



## Revision of the giant geckos of New Caledonia (Reptilia: Diplodactylidae: *Rhacodactylus*)

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### Abstract

We employed a molecular phylogenetic approach using the mitochondrial ND2 gene and five associated tRNAs (tryptophan, alanine, asparagine, cysteine, tyrosine) and the nuclear RAG1 gene to investigate relationships within the diplodactylid geckos of New Caledonia and particularly among the giant geckos, *Rhacodactylus*, a charismatic group of lizards that are extremely popular among herpetoculturalists. The current generic allocation of species within New Caledonian diplodactylids does not adequately reflect their phylogenetic relationships. *Bavayia madjo*, a high-elevation endemic is not closely related to other *Bavayia* or to members of any other genus and is placed in a new genus, *Paniegekko* **gen. nov.** *Rhacodactylus* is not monophyletic. The small-bodied and highly autapomorphic genus *Eurydactylodes* is embedded within *Rhacodactylus* as sister to *R. chahoua*. *Rhacodactylus ciliatus* and *R. sarasinorum* are sister taxa but are not part of the same clade as other giant geckos and the generic name *Correlophus* Guichenot is resurrected for them. Remaining New Caledonian giant geckos (*R. leachianus*, *R. trachrhynchus*, *R. auriculatus*) receive weak support as a monophyletic group. Although the monophyly of *Rhacodactylus* (including *Eurydactylodes*) exclusive of *Correlophus* cannot be rejected, our results support the recognition of a *R. chahoua* + *Eurydactylodes* clade separate from *Rhacodactylus sensu stricto*. Because of the distinctiveness of *Eurydactylodes* from *R. chahoua* (and other New Caledonian ‘giant geckos’), we retain this name for the four species to which it has been consistently applied and erect a new genus, *Mniarogekko* **gen. nov.** to accommodate *R. chahoua*. There is little genetic differentiation within the narrowly distributed *Correlophus sarasinorum*, but *C. ciliatus* from southern New Caledonia are both genetically and morphologically differentiated from a recently discovered *Correlophus* from the Îles Belep, north of the Grande Terre, which is here described as *C. belepensis* **sp. nov.** Although only subtly different morphologically, the populations of *Mniarogekko* from the far northwest of the Grande Terre and from the Îles Belep are strongly differentiated genetically from *M. chahoua* populations in the central part of the Grande Terre and are described as *M. jalu* **sp. nov.** *Rhacodactylus auriculatus* exhibits some genetic substructure across its nearly island-wide range in New Caledonia, but overall divergence is minimal. *Rhacodactylus leachianus* exhibits low levels of divergence across its range and southern insular forms previously assigned to *R. l. henkeli* are not divergent from southern Grande Terre populations. The few populations of *R. trachrhynchus* sampled are strongly divergent from one another and a specimen from Îlot Môrô near the Île des Pins is especially distinctive. This specimen and others examined from Îlot Môrô are morphologically assignable to the species described by Boulenger in 1878 as *Chameleonurus trachycephalus* and is recognized here as a full species. New diagnoses are provided for each of the eight genera of endemic New Caledonian diplodactylid geckos now recognized. The results of our study necessitate determinations of the conservation status of the new species described or recognized. *Mniarogekko jalu* **sp. nov.** is considered Endangered, but is locally abundant. *Correlophus belepensis* **sp. nov.** is considered Critically Endangered and is restricted to the ultramafic plateaux of Île Art. Although described from the Île des Pins, we have only been able to confirm the existence of *Rhacodactylus trachycephalus* on the tiny satellite island Îlot Môrô and consider it to be Critically Endangered. If indeed restricted to this islet, *R. trachycephalus* may well have the smallest range and perhaps the smallest population of any gecko in the world.

**Key words:** Squamata, *Rhacodactylus*, *Correlophus*, *Mniarogekko* **gen. nov.**, *Paniegekko* **gen. nov.**, *Correlophus belepensis* **sp. nov.**, *Mniarogekko jalu* **sp. nov.**, New Caledonia, molecular phylogenetics, conservation

## Introduction

The biota of New Caledonia is both phylogenetically and ecologically diverse and is noted for its high level of endemism (Holloway 1979; Chazeau 1993), and the New Caledonian region has been identified as one of the world's hotspots of tropical biodiversity (Myers 1988, 1990; Mittermeier *et al.* 1996; Myers *et al.* 2000; Lowry *et al.* 2004). Among terrestrial vertebrates, lizards constitute the most diverse and highly-endemic component of the fauna (Bauer 1989, 1999; Bauer & Sadlier 2000; Smith *et al.* 2007). The indigenous lizard fauna is dominated by iguanomorphine skinks and diplodactylid geckos. The best known and perhaps the most distinctive of the New Caledonian geckos, and among the most noteworthy of all geckos, are the members of the genus *Rhacodactylus* Fitzinger, 1843. The genus includes the two largest living species of geckos (Russell & Bauer 1986), the only viviparous geckos outside of New Zealand (Bartmann & Minuth 1979), and perhaps the most saurophagous of all geckos (Snyder *et al.* 2010). While biological data on members of the genus remains limited (Bauer & Sadlier 2000; Henkel 2009; Snyder *et al.* 2010), all six recognized species are regularly kept in captivity and there exists a voluminous literature associated with their captive care and breeding (Tytte 1992; Seipp & Henkel 2000, 2011; Tröger 2001; de Vosjoli *et al.* 2003; Henkel & Schmidt 2007; Cemelli 2009; Schönecker & Schönecker 2009a, *inter alia*). On the one hand, the success of these species in captivity and the ease with which at least some species can be kept and bred has probably decreased demand for wild caught individuals in the pet trade and brought a global awareness to the uniqueness of these geckos. On the other hand, popular awareness of attractive color morphs and 'varieties' may drive illegal collection of *Rhacodactylus*, particularly those species that have proven more difficult to breed in captivity.

Despite being represented by only six species, the genus has had a relatively complex and convoluted taxonomic history. Perhaps more than most geckos, individual species of *Rhacodactylus* are highly distinctive and early workers placed the few species into four genera: *Rhacodactylus* Fitzinger, 1843, *Correlophus* Guichenot, 1866, *Ceratolophus* Bocage, 1873, and *Chameleonurus* Boulenger, 1878. The generic revision of Boulenger (1883) stabilized the nomenclature of the group, synonymizing the known forms into five species in a single genus. In 1913 a sixth species, *R. sarasinorum*, was described by Roux. Composition of the genus has remained relatively stable, although two non-nominate subspecies of *R. leachianus* (Cuvier, 1829), *R. l. aubrianus* Bocage, 1873 and *R. l. henkeli* Seipp & Obst, 1994, and one of the live-bearing *R. trachyrhynchus* Bocage, 1873, *R. t. trachycephalus* (Boulenger, 1878), have been variously recognized by some authors (e.g., Kluge 2001; Seipp & Henkel 2011). Bauer (1990; Bauer & Henle 1994) recognized the three species of *Pseudothecadactylus* Brongersma, 1936, a northern Australian genus, as subgenerically distinct within *Rhacodactylus*, based on a morphologically-derived phylogeny. However, subsequent molecular evidence has confirmed that this group is outside the New Caledonian diplodactylid radiation (Bauer & Jackman 2006) and is probably its immediate sister group (Nielsen *et al.* 2011); as such it will not be discussed further here.

Although representative *Rhacodactylus* have been included in a number of molecular phylogenetic analyses (e.g., Donnellan *et al.* 1999; Oliver & Sanders 2009), phylogenetic analyses of the genus as a whole have been limited. Bauer (1990) and Bauer *et al.* (1993) using morphological data only, recovered *R. auriculatus* (Bavay, 1869) as the sister to all remaining species and *R. chahoua* (Bavay, 1869) and *R. ciliatus* (Guichenot, 1866) as sister taxa. The more recent of these analyses placed *R. sarasinorum* as sister to the *chahoua* + *ciliatus* pair, with *leachianus* + *trachyrhynchus* as sister to this clade. Both Bauer (1990) and Good *et al.* (1997; see also Bauer & Sadlier 2000), using allozyme data plus morphology, found *sarasinorum* and *trachyrhynchus* as sister taxa and placed *leachianus* as the sister to the *chahoua* + *ciliatus* pair.

In the first analysis based on DNA sequence data, Vences *et al.* (2001) used a 513 bp fragment of the 16S mitochondrial gene to elucidate relationships. They found low support for the monophyly of the genus and the only supraspecific clusters receiving ML bootstrap support of greater than 70% were *R. ciliatus* + *R. sarasinorum* (85%) and this clade + *R. chahoua*. They also found quite deep divergence between southern mainland + insular populations of *R. leachianus* and those on the northern mainland, but little divergence between insular and mainland *R. trachyrhynchus*. Patterns of implied species' relationships differed in each of their analyses (neighbor-joining, maximum parsimony, maximum likelihood). Bauer *et al.* (2004, 2009) and Bauer and Jackman (2006) presented preliminary data on relationships of New Caledonian diplodactylids and indicated that data from a combination of nuclear and mitochondrial genes strongly suggested that *Rhacodactylus* was made paraphyletic by *Eurydactylodes* (not included in the study of Vences *et al.* 2001), which was found to be the sister to *R. chahoua*.

Bauer *et al.* (2004) also noted that *R. sarasinorum* and *R. ciliatus* were strongly supported as sister taxa and that they found no support for the genetic distinctiveness of *R. l. henkeli*. Bauer and colleagues, however, did not publish their explicit trees for New Caledonian diplodactylids at that time.

Thus, each of the previous studies of *Rhacodactylus* has supported a different pattern of interspecific relationships, and there has been no agreement even upon the monophyly of the group. We employed a taxon complete, multi-gene approach with representative intra-specific sampling to evaluate phylogenetic patterns within *Rhacodactylus*. Specifically, we investigated 1) the monophyly of *Rhacodactylus*, 2) the pattern of species-level relationships, 3) the validity of the subspecies *R. l. henkeli* and *R. t. trachycephalus*, and 4) the relationship of recently discovered disjunct populations resembling *R. chahoua*, *R. ciliatus*, and *R. auriculatus* (Whitaker *et al.* 2004; Bauer *et al.* 2006a,b). Of necessity, these objectives required us to reevaluate phylogenetic relationships among all new Caledonian diplodactylids and our findings have led us to propose a new generic level classification for this clade.

## Materials and methods

**Specimens.** The majority of specimens examined (Appendix), as well as those from which DNA sequences were obtained (Table 1), are housed in the collections of the Australian Museum, Sydney (AMS) and the California Academy of Sciences, San Francisco (CAS and CAS-SU). Additional *Rhacodactylus* and outgroup specimens were cited or examined (and in some cases sequenced) from the following collections and institutions: Aaron M. Bauer collection, Villanova (AMB), American Museum of Natural History, New York (AMNH), The Natural History Museum, London (BMNH), Monty L. Bean Museum, Brigham Young University, Provo (BYUH), Musée de l'École de Médecine Navale, Brest [no longer in existence] (EMNB), Field Museum of Natural History, Chicago (FMNH), Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSNB), Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ), Muséum d'Histoire Naturelle, Gèneve (MHNG), Museu de Lisboa, Lisbon [destroyed by fire] (MLI), Musée d'Histoire Naturelle, Marseille (MMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), Museum für Tierkunde, Senckenberg Naturhistorische Sammlungen, Dresden (MTKD), Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), Naturhistoriska Riksmuseet, Göteborg (NHMG), Naturhistorisches Museum Basel (NMB), Naturhistorisches Museum, Wien (NMW), Naturalis–Nationaal Natuurhistorisch Museum, Leiden (RMNH), Royal Ontario Museum, Toronto (ROM), Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main (SMF), University of Michigan Museum of Zoology, Ann Arbor (UMMZ), United States National Museum of Natural History, Washington, DC (USNM), Yale Peabody Museum of Natural History, New Haven (YPM), Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK), Zoological Institute, Russian Academy of Sciences, St. Petersburg [formerly ZIL] (ZIN), Zoological Museum Hamburg (ZMH), and Zoologische Sammlung der Bayerischen Staates, München (ZSM).

**Morphology.** Specimens were examined under a Nikon SMZ 1000 binocular microscope and photographs were taken with a Canon G11 Powershot digital camera. The following measurements were taken with digital calipers (to the nearest 0.1 mm): snout-vent length (SVL; from tip of snout to vent), trunk length (TrunkL; distance from axilla to groin measured from posterior edge of forelimb insertion to anterior edge of hindlimb insertion, with limbs at right angles to the body axis), forearm length (ForeaL; from base of palm to elbow, with limb partially flexed); crus length (CrusL; from base of heel to knee, with limb partially flexed); tail length (TailL; from vent to tip of tail), tail width (TailW; measured at widest point of tail); head length (HeadL; distance between posterior margin of retroarticular process of jaw and snout-tip), head width (HeadW; maximum width of head), ear length (EarL; longest dimension of ear); orbital diameter (OrbD; greatest diameter of orbit), naris to eye distance (NarEye; distance between anteriormost point of eye and posteriormost point of nostril), snout to eye distance (SnEye; distance between anteriormost point of eye and tip of snout), eye to ear distance (EyeEar; distance from anterior edge of ear opening to posterior corner of eye), internarial distance (Internar; distance between nares), and interorbital distance (Interorb; shortest distance between left and right supraciliary scale rows). Unless otherwise stated, measurements were made on right side of specimens. Number of supralabials (and number to midpoint of eye) (SupraL), infralabials (InfraL), and lamellae under digits of the manus (LamManus) and pes (LamPes) were recorded bilaterally. Digital X-ray images of specimens were obtained using a Faxitron closed cabinet X-ray (LX-60, Faxitron Corp.) with a Varian flat-panel digital X-ray detector.

**TABLE 1.** Specimens used in the molecular phylogeny of New Caledonian diplodactylids. See Materials and methods for a list of museum and other acronyms/codes used. Under locality NC = New Caledonia, NZ = New Zealand and AUS = Australia. Latitudes and longitudes are provided for New Caledonian giant geckos (*Correlophus*, *Mniarogekko*, *Rhacodactylus*) only. Numbers following species names correspond to those used to differentiate conspecific samples in Figure 1.

Species	Specimen Number	Locality	Latitude (° S)	Longitude (° E)	GenBank Numbers	
					ND2+rRNAs	RAG1
<i>Correlophus belepensis</i> <b>sp. nov.</b> 1	MNHN 2011.1100	NC, Îles Belep, Île Art, 2 km E Waala, Wèné Cogat	19.7130	163.6605	JX024437	JX024478
<i>Correlophus belepensis</i> <b>sp. nov.</b> 2	AMS R161283	NC, Îles Belep, Île Art, 2 km E Waala, Wèné Cogat	19.7130	163.6605	JX024436	JX024477
<i>Correlophus ciliatus</i> 2	No data (captive)	NC, Île des Pins (no precise locality)			JX024443	–
<i>Correlophus ciliatus</i> 3	AMS R146594	NC, Rivière Bleue, vic. Pont Germain	22.1000	166.6333	JX024439	EF534778
<i>Correlophus ciliatus</i> 4	AMS R146595	NC, Rivière Bleue, vic. Pont Germain	22.1000	166.6333	JX024438	JX024480
<i>Correlophus ciliatus</i> 6	CAS 205458	NC, Rivière Bleue, vic. Pont Germain	22.1000	166.6333	JX024441	JX024481
<i>Correlophus ciliatus</i> 5	CAS 205482	NC, Rivière Bleue, vic. Pont Germain	22.1000	166.6333	JX024442	JX024482
<i>Correlophus ciliatus</i> 1	AMS R150736	NC, Mt. Dzumac	22.0333	166.4500	JX024440	JX024479
<i>Correlophus sarasinorum</i> 10	AMS R150019	NC, Plaine des Lacs, Kwa Néie	22.3153	166.9131	JX024459	JX024483
<i>Correlophus sarasinorum</i> 7	AMS R150021	NC, Plaine des Lacs, Kwa Néie	22.3153	166.9131	JX024460	JX024484
<i>Correlophus sarasinorum</i> 9	AMS R150022	NC, Plaine des Lacs, Kwa Néie	22.3153	166.9131	JX024461	–
<i>Correlophus sarasinorum</i> 6	AMS R150023	NC, Plaine des Lacs, Kwa Néie	22.3153	166.9131	JX024458	JX024485
<i>Correlophus sarasinorum</i> 8	AMS R150027	NC, Plaine des Lacs, Forêt Nord on SW base of Kwa Néie	22.3244	166.9142	JX024455	–
<i>Correlophus sarasinorum</i> 2	AMS R161920	NC, Le Bois de Sud	22.1728	166.7647	JX024453	JX024487
<i>Correlophus sarasinorum</i> 1	CAS 205422	NC, Mt. Koghis	22.1786	166.5056	JX024461	–
<i>Correlophus sarasinorum</i> 4	AMS R152658	NC, Mt. Koghis	22.1786	166.5056	JX024452	JX024486
<i>Correlophus sarasinorum</i> 3	CAS 205421	NC, Mt. Koghis	22.1786	166.5056	JX024460	–
<i>Correlophus sarasinorum</i> 5	CAS 157675	NC, 1 km S Touaourou	22.2208	166.9839	JX024454	JX024488
<i>Mniarogekko chahoua</i> 1	AMS R144171	NC, Sarraméa	21.6333	165.8333	JX024432	JX024505
<i>Mniarogekko chahoua</i> 2	CAS 156691	NC, St. Therese, 15 km NE Poindimié, Vallée d'Amoa	20.9667	165.2222	JX024433	JX024506
<i>Mniarogekko jalu</i> <b>sp. nov.</b> 3	CAS 250859	NC, 15 km N Koumac, Rivière Néhoué	20.4194	164.2212	JX024429	–
<i>Mniarogekko jalu</i> <b>sp. nov.</b> 6	AMS R161224	NC, 24 km N Koumac, Forêt d'Ougne, Vallée Poupoule	20.3344	164.2853	DQ533741	JX024508
<i>Mniarogekko jalu</i> <b>sp. nov.</b> 2	AMS R161237	NC, 11 km NW Koumac, Dôme de Tiébaghi	20.4578	164.1897	JX024434	–
<i>Mniarogekko jalu</i> <b>sp. nov.</b> 1	AMS R161238	NC, 11 km NW Koumac, Dôme de Tiébaghi	20.4578	164.1897	JX024435	JQ173759
<i>Mniarogekko jalu</i> <b>sp. nov.</b> 4	AMS 161286	NC, Îles Belep, Île Art, 2 km E Waala, Wèné Cogat	19.7130	163.6605	JX024430	–
<i>Mniarogekko jalu</i> <b>sp. nov.</b> 5	AMS 161287	NC, Îles Belep, Île Art, 2 km E Waala, Wèné Cogat	19.7130	163.6605	JX024431	JX024507
<i>Rhacodactylus auriculatus</i> 20	CAS 250847	NC, Pic Ningua	22.0236	166.4700	JX024405	JX024540
<i>Rhacodactylus auriculatus</i> 19	CAS 250848	NC, Mt. Ouin	22.0194	166.4717	JX024406	JX024541

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TABLE 1. (Continued)

Species	Specimen Number	Locality	Latitude (° S)	Longitude (° E)	GenBank Numbers	
					ND2+tRNAs	RAG1
<i>Rhacodactylus auriculatus</i> 33	CAS 250849	NC, Mt. Gouémba (= Wó Bwa Wíwá)	22.1667	166.9408	JX024395	JX024535
<i>Rhacodactylus auriculatus</i> 52	CAS 250851	NC, Mt. Gouémba (= Wó Bwa Wíwá)	22.1667	166.9408	JX024407	JX024542
<i>Rhacodactylus auriculatus</i> 47	CAS 250853	NC, Mt. Gouémba (= Wó Bwa Wíwá)	22.1667	166.9408	JX024408	JX024543
<i>Rhacodactylus auriculatus</i> 16	CAS 250854	NC, Pic Ningua	21.7433	166.1506	JX024396	JX024536
<i>Rhacodactylus auriculatus</i> 11	CAS 250855	NC, Pic Ningua	21.7433	166.1506	JX024409	JX024544
<i>Rhacodactylus auriculatus</i> 15	CAS 250857	NC, Pic Ningua	21.7403	166.1558	JX024410	JX024545
<i>Rhacodactylus auriculatus</i> 21	AMS R146593	NC, Rivière Bleue, vic. Giant Kauri	22.1000	166.6667	JX024387	JX024511
<i>Rhacodactylus auriculatus</i> 29	AMS R146446	NC, 1.3 km from summit of Mt. Do	21.7597	165.9967	JX024386	–
<i>Rhacodactylus auriculatus</i> 31	AMS R146447	NC, 2.6 km from summit of Mt. Do	21.7667	166.0042	JX024384	–
<i>Rhacodactylus auriculatus</i> 30	AMS R146448	NC, 2.2 km from summit of Mt. Do	21.7667	166.0042	JX024385	–
<i>Rhacodactylus auriculatus</i> 23	AMS R152645	NC, Plaine des Lacs, K wa Néie	22.3153	166.9131	JX024377	JX024512
<i>Rhacodactylus auriculatus</i> 49	AMS R152646	NC, Plaine des Lacs, K wa Néie	22.3153	166.9131	JX024411	JX024513
<i>Rhacodactylus auriculatus</i> 46	AMS R152647	NC, Plaine des Lacs, K wa Néie	22.3153	166.9131	JX024412	JX024514
<i>Rhacodactylus auriculatus</i> 18	AMS R152649	NC, Plaine des Lacs, K wa Néie	22.3153	166.9131	JX024413	JX024515
<i>Rhacodactylus auriculatus</i> 22	AMS R152650	NC, Plaine des Lacs, K wa Néie	22.3153	166.9131	JX024378	JX024516
<i>Rhacodactylus auriculatus</i> 8	AMS R161093	NC, Mt. Kaala, 6 km N Kaala-Gomen, headwaters of Oué Injob	20.6175	164.3803	JX024381	–
<i>Rhacodactylus auriculatus</i> 7	AMS R161094	NC, Mt. Kaala, 6 km N Kaala-Gomen, headwaters of Oué Injob	20.6175	164.3803	JX024382	JX024517
<i>Rhacodactylus auriculatus</i> 6	AMS R161117	NC, Massif de Koniambo, 8 km NE Koné, headwaters of Rivière Pandanus	20.9975	164.8131	JX024383	JX024518
<i>Rhacodactylus auriculatus</i> 2	AMS R161251	NC, Dôme de Tiébaghi, 14 km NW Koumac	20.4606	164.1864	JX024427	JX024519
<i>Rhacodactylus auriculatus</i> 1	AMS R161252	NC, Dôme de Tiébaghi, 14 km NW Koumac	20.4606	164.1864	JF972429	–
<i>Rhacodactylus auriculatus</i> 3	AMS R161253	NC, Dôme de Tiébaghi, 14 km NW Koumac	20.4606	164.1864	JX024428	JX024520
<i>Rhacodactylus auriculatus</i> 5	AMS R163166	NC, Plateau de Tia, S Pouembout	21.1825	164.8844	JX024379	JX024521
<i>Rhacodactylus auriculatus</i> 4	AMS R163182	NC, Massif du Boulinda, 1.5 km SW Mt. Boulinda	21.2642	165.1411	JX024380	JX024522
<i>Rhacodactylus auriculatus</i> 10	AMS R171233	NC, Pic Ningua	21.7242	166.1367	JX024420	JX024523
<i>Rhacodactylus auriculatus</i> 9	AMS R171242	NC, Pic Ningua	21.7419	166.1556	JX024421	JX024524
<i>Rhacodactylus auriculatus</i> 26	CAS 157676	NC, Touaourou, 6 km S Gite St. Gabriel	22.2536	167.0056	JX024388	JX024525
<i>Rhacodactylus auriculatus</i> 24	CAS 157678	NC, Touaourou, 5 km S Gite St. Gabriel	22.2542	167.0056	JX024390	–
<i>Rhacodactylus auriculatus</i> 25	CAS 165901	NC, Touaourou, 5 km S Gite St. Gabriel	22.2542	167.0056	JX024389	–
<i>Rhacodactylus auriculatus</i> 44	CAS 157679	NC, Touaourou, 1 km S	22.2222	166.9889	JX024391	JX024526

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TABLE 1. (Continued)

Species	Specimen Number	Locality	Latitude (° S)	Longitude (° E)	GenBank Numbers	
					ND2+rRNAs	RAG1
<i>Rhacodactylus auriculatus</i> 45	CAS 157681	NC, Touaourou, 1 km S	22.2222	166.9889	JX024392	JX024527
<i>Rhacodactylus auriculatus</i> 27	CAS 205429	NC, Rivière Bleue, vic. Pont Germain	22.1028	166.6528	JX024393	JX024533
<i>Rhacodactylus auriculatus</i> 28	CAS 205431	NC, Rivière Bleue, vic. Pont Germain	22.1028	166.6528	JX024394	JX024534
<i>Rhacodactylus auriculatus</i> 43	CAS 205432	NC, Rivière Bleue, vic. Pont Germain	22.1028	166.6528	JX024397	JX024528
<i>Rhacodactylus auriculatus</i> 51	CAS 205433	NC, Rivière Bleue, vic. Pont Germain	22.1028	166.6528	JX024398	JX024529
<i>Rhacodactylus auriculatus</i> 34	CAS 205434	NC, Rivière Bleue, vic. Pont Germain	22.1028	166.6528	JX024399	JX024530
<i>Rhacodactylus auriculatus</i> 32	CAS 205435	NC, Rivière Bleue, vic. Pont Germain	22.1028	166.6528	JX024400	JX024531
<i>Rhacodactylus auriculatus</i> 39	CAS 205438	NC, Rivière Bleue, vic. Pont Germain	22.1028	166.6528	JX024401	JX024532
<i>Rhacodactylus auriculatus</i> 48	CAS 205484	NC, Plaine des Lacs, Kwa Néie	22.3153	166.9131	JX024402	JX024537
<i>Rhacodactylus auriculatus</i> 53	CAS 205485	NC, Plaine des Lacs, Kwa Néie	22.3153	166.9131	JX024403	JX024538
<i>Rhacodactylus auriculatus</i> 36	EBU 50509	NC, 'La Locomobile', Rivière Bleue	22.1514	166.6793	JX024416	JX024548
<i>Rhacodactylus auriculatus</i> 35	EBU 50510	NC, 'La Locomobile', Rivière Bleue	22.1514	166.6793	JX024417	JX024549
<i>Rhacodactylus auriculatus</i> 37	EBU 50511	NC, 'La Locomobile', Rivière Bleue	22.1514	166.6793	JX024418	JX024550
<i>Rhacodactylus auriculatus</i> 38	EBU 50512	NC, 'La Locomobile', Rivière Bleue	22.1514	166.6793	JX024419	JX024551
<i>Rhacodactylus auriculatus</i> 41	EBU 50455	NC, Rivière des Pirogues	22.2585	166.6961	JX024414	JX024546
<i>Rhacodactylus auriculatus</i> 17	EBU 50456	NC, Rivière des Pirogues	22.2585	166.6961	JX024415	JX024547
<i>Rhacodactylus auriculatus</i> 14	EBU 62960	NC, Chetorè Kwèdè, Haut Nakéty, 8km E Nakéty	21.5509	166.1120	JX024422	–
<i>Rhacodactylus auriculatus</i> 13	EBU 62962	NC, Bwaako, Presqu'île Bogota	21.4811	166.0146	JX024423	–
<i>Rhacodactylus auriculatus</i> 12	EBU 62978	NC, Kotabo, Presqu'île Bogota	21.5048	166.0280	JX024424	–
<i>Rhacodactylus auriculatus</i> 42	EBU 63863	NC, Chutes de la Madéléine	22.2306	166.8600	JX024425	–
<i>Rhacodactylus auriculatus</i> 40	EBU 63864	NC, Chutes de la Madéléine	22.2306	166.8600	JX024426	–
<i>Rhacodactylus auriculatus</i> 50	CAS 205486	NC, Plaine des Lacs, Kwa Néie	22.3153	166.9131	JX024404	JX024539
<i>Rhacodactylus leachianus</i> 8	CAS 250842	NC, Îlot Môrô	22.6542	167.3931	GU459949	GU459548
<i>Rhacodactylus leachianus</i> 9	CAS 250843	NC, Îlot Môrô	22.6542	167.3931	JX024448	JX024557
<i>Rhacodactylus leachianus</i> 4	CAS 250860	NC, vicinity Goro	22.2875	167.0111	JX024449	JX024558
<i>Rhacodactylus leachianus</i> 2	AMS R146420	NC, Mt. Aoupinié	21.1553	165.3200	JX024446	JX024553
<i>Rhacodactylus leachianus</i> 5	AMS R152651	NC, Plaine des Lacs, Kwa Néie	22.3153	166.9131	JX024444	JX024554
<i>Rhacodactylus leachianus</i> 1	CAS 165890	NC, Vallée de Nimbaye, near Ponérihouen	21.1000	165.3500	JX024445	JX024555

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TABLE 1. (Continued)

Species	Specimen Number	Locality	Latitude (°S)	Longitude (°E)	GenBank Numbers	
					ND2+rRNAs	RAG1
<i>Rhacodactylus leachianus</i> 7	CAS 214446	NC, Îlot Bayonnaise	22.6692	167.4233	JX024447	JX024556
<i>Rhacodactylus leachianus</i> 6	No Data (captive)	? [presumably Île des Pins or surrounding islands]			JX024451	JX024552
<i>Rhacodactylus leachianus</i> 3	YPM 14621	NC, Col d'Tonghoue:	22.1917	166.4792	JX024450	–
<i>Rhacodactylus trachyrhynchus</i>	CAS 214440	NC, Îlot Môrô	22.6508	167.3931	JX024465	JX024559
<i>Rhacodactylus trachyrhynchus</i> 2	AMS R146418	NC, Mt. Aoupinié	21.1553	165.3200	JX024464	JX024560
<i>Rhacodactylus trachyrhynchus</i> 3	AMS R146419	NC, Mt. Aoupinié	21.1553	165.3200	JX024462	JX024561
<i>Rhacodactylus trachyrhynchus</i> 1	CAS 200269	NC, Pindai	21.3339	164.9725	JX024463	JX024562
<i>Carphodactylus laevis</i>	AMS R143258	AUS, Queensland, Lamb Range			GU459943	GU459542
<i>Crenadactylus ocellatus</i>	SAMA R22245	AUS, Northern Territory, 10 km S Barrow Creek			JX024364	JX024489
<i>Diplodactylus conspicillatus</i>	AMS R158426	AUS, NSW, Sturt National Park			JX024358	JQ173721
<i>Diplodactylus granariensis</i>	AMS R150637	AUS, Western Australia, Dedari			JX024359	JX024498
<i>Strophurus assimilis</i>	AMS R149832	AUS, Western Australia, 3.8 km N Bonny Vale			JX024360	JQ173760
<i>Strophurus intermedius</i>	AMS R158434	AUS, NSW, 35km from Mt. Hope on Euabalong Road			GU459952	GU459551
<i>Oedura marmorata</i>	AMS R143861	AUS, Queensland, Stonehenge area			GU459951	GU459550
<i>Oedura rhombifer</i>	AMS R136216	AUS, Northern Territory, 3.5 km upstream from Bells Gorge			JX024363	JX024509
<i>Lucasium maini</i>	AMS R150647	AUS, Western Australia, Dedari			JX024362	JX024503
<i>Lucasium stendodactylum</i>	AMS R139897	AUS, Western Australia, El Questro Station			JX024361	JX024504
<i>Rhynchoedura ornata</i>	AMS R155371	AUS, NSW, Sturt National Park			GU459954	JX024563
<i>Woodworthia chrysoisireticus</i>	RAH 476	NZ, Mana Is.			GU459841	GU459438
<i>Woodworthia maculata</i>	RAH 292	NZ, Titahi Bay			GU459852	GU459449
<i>Mokopirirakau granulatus</i>	RAH 66	NZ, Northcross			GU459817	GU459414
<i>Mokopirirakau granulatus</i>	RAH 90	NZ, Bethels Beach			GU459818	GU459415
<i>Naultinus gemmeus</i>	RAH 464	NZ, Hakataramea Pass			GU459764	GU459361
<i>Naultinus grayi</i>	RAH 253	NZ, Kaimaumu Swamp			GU459766	GU459363
<i>Pseudothecadactylus australis</i>	QMJ 157120	AUS, north Queensland			JX024365	JX024510
<i>Pseudothecadactylus lindneri</i>	MVZ 99544	AUS, Northern Territory, Kakadu National Park			GU459946	GU459545
<i>Bavayia crassicollis</i>	AMS R163392	NC, Loyalty Islands, Lifou, Luceilla			JX024366	JX024466
<i>Bavayia cyclura</i>	CAS 157697	NC, Plage de Poé			JX024367	JX024467
<i>Bavayia robusta</i>	NR 4696	NC, Mt. Koghis			JX024372	JX024474

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TABLE 1. (Continued)

Species	Specimen Number	Locality	Latitude		Longitude		GenBank Numbers	
			(°S)	(°E)	(°S)	(°E)	ND2+rRNAs	RAG1
<i>Bavayia montana</i>	AMS R144235	NC, Mt. Panié					JX024370	JX024471
<i>Bavayia goroensis</i>	AMS R166030	NC, Plaine Des Laes, Route De La Wajana					EU054303	JX024470
<i>Bavayia ornata</i>	AMS R149306	NC, Mt. Panié					DQ533737	JX024472
<i>Bavayia septuiclavus</i>	CAS 205439	NC, Rivière Bleue, vic. Pont Germain					JX024374	JX024476
<i>Bavayia exsuccida</i>	AMS R150668	NC, Pindai					JX024368	JX024468
<i>Bavayia geitaina</i>	AMS R152661	NC, Mt. Koghis					JX024369	JX024469
<i>Bavayia pulchella</i>	AMS R149935	NC, Ranges west of Mé Adéo					JX024371	JX024473
<i>Bavayia savagii</i>	AMS R144318	NC, Mt. Koghis					JX024373	JX024475
<i>Eurydactyloides agricolae</i>	AMS R161111	SMGM Mine, south side Piton de Pandop, massif Kaala					DQ533746	JX024499
<i>Eurydactyloides symmetricus</i>	CAS 205477	NC, Rivière Bleue, vic. Pont Germain					DQ533742	JX024501
<i>Eurydactyloides vieillardii</i>	AMS R149485	NC, Forêt Plate					DQ533773	JX024502
<i>Eurydactyloides occidentalis</i>	AMS R166218	NC, Marais Fournier, Mouéara, Gouaro-Déva					DQ533776	JX024500
<i>Oedodera marmorata</i>	AMS R161254	Creek à Paul, Sommet Noir, Paagoumène, 11 km, NW Koumac					AY858957	JQ173726
<i>Pantiegekko madjo</i>	AMS R149329	NC, Mt. Panié					GU459950	GU459549
<i>Dierogekko inexpectatus</i>	AMS R175527	NC, Paevala, Sommet Poun					JF972439	JX024490
<i>Dierogekko poumensis</i>	AMS R161205	NC, Sommet Poun, 3 km S Poun					JX024375	JX024495
<i>Dierogekko thomaswhitei</i>	AMS R161153	NC, Gomen Mine, Mt Taom, Massif d'Ouazangou-Taom					JX024376	JX024496
<i>Dierogekko insularis</i>	AMS R161066	NC, Pânan, Île Pott, Îles Belep					JF972459	JX024491
<i>Dierogekko koniambo</i>	AMS R161129	NC, Headwaters of Rivière Pandanus, Massif de Koniambo					JF972451	JX024493
<i>Dierogekko kaalaensis</i>	AMS R161101	NC, East side Piton de Pandop, massif Kaala					JF972454	JX024492
<i>Dierogekko validiclavus</i>	AMS R144230	NC, Mt. Panié					JF972461	JX024497
<i>Dierogekko nehoueensis</i>	CAS 231835	NC, Rivière Néhoué					JF972438	JX024494
<i>Lialis burtonis</i>	JFBM8	captive (no data)					JX024354	GU459540
<i>Paradelma orientalis</i>	SAMO932	AUS					AY134605	HQ426304
<i>Pygopus lepidopodus</i>	WBJ1206	AUS, Western Australia, Lesueur National Park					AY134603	HQ426319
<i>Pygopus nigriceps</i>	MVZ 197233	AUS, Northern Territory, 81 km S Alice springs					JX024355	EF534783
<i>Nephrurus levis</i>	AMS R140561	AUS, Western Australia, Denham					GU459945	GU459544
<i>Saltuarius swaini</i>	AMS R143262	AUS, Queensland, Lamb Range					JX024356	JQ945338
<i>Phyllurus platurus</i>	AMB42	AUS, New South Wales, Sydney					JX024357	HQ426314

**Molecular methods.** Nucleotide sequences from the mitochondrial ND2 and five flanking tRNAs (tryptophan, alanine, asparagine, cysteine, tyrosine), and from the nuclear RAG1 genes were obtained from representatives of all described genera and species of New Caledonian diplodactylid geckos (except the recently described *Bavayia nubila* Bauer, Sadlier, Jackman & Shea, 2012, which is the sister species to *B. goroensis* Bauer, Jackman, Sadlier, Shea & Whitaker, 2008. In addition, representative New Zealand and Australian diplodactylids, including two species of *Pseudothecadactylus* — the immediate sister group to the New Caledonian clade — and representatives of the Carphodactylidae and Pygopodidae were included as outgroup taxa. In total 2286 bp of sequence were generated for 144 pygopodoid gecko samples including 25 outgroup taxa and 34 taxa of New Caledonian diplodactylids (Table 1). Genomic DNA was extracted using the Qiagen QIAmp tissue kit and PCR amplification was conducted under a variety of thermocycler parameters using a diversity of primers (see Nielsen *et al.* 2011 for detailed primer information and PCR conditions). Products were visualized via 1.5% agarose gel electrophoresis. Amplified products were purified either using an AmPure magnetic bead PCR purification kit or reamplified products were purified on 2.5% acrylamide gels (Maniatis *et al.*, 1982) after being reamplified from 2.5% low-melt agarose plugs. DNA from acrylamide gels was eluted from the acrylamide passively over two days with Maniatis elution buffer (Maniatis *et al.* 1982). Cycle-sequencing reactions were performed using the Applied Biosystems BigDye™ primer cycle sequencing ready reaction kit. The resulting products were purified using SeqClean magnetic bead purification kit. Purified sequencing reactions were analyzed on an ABI 373A stretch gel sequencer or an ABI 3700 automated sequencer. To ensure accuracy, negative controls were included in every reaction, complementary strands were sequenced, and sequences were manually aligned using the original chromatograph data in the program SeqMan II. Sequences have been deposited in GenBank (Table 1).

**Phylogenetic methods.** Phylogenetic trees were estimated using maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI). PAUP\* 4.0b10a (Swofford 2002) was used to estimate parsimony trees. Parsimony searches were conducted with 100 heuristic searches using random addition of sequences. Non-parametric bootstrap resampling was used to assess support for individual nodes using 1000 bootstrap replicates with ten random addition searches. For maximum likelihood analyses, a partitioned RAXML 7.2.6 (Stamatakis 2006) analysis with the General Time Reversible plus Gamma model was used with a 7 partition analysis (3 mitochondrial codon positions, 3 nuclear codon positions, and 1 tRNA partition). The best tree was estimated from 100 runs and 1000 bootstrap replicates were performed with bootstrap percentages associated with the best maximum likelihood tree and the branch lengths associated with the best tree. To estimate a phylogenetic tree with a Bayesian framework MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) was used with the model chosen using ModelTest 3.7. (Posada & Crandall 1998) using the seven partition analysis described above. The Bayesian analyses were initiated from random starting trees and run for 10,000,000 generations with four incrementally-heated Markov chains. Likelihood parameter values were estimated from the data and initiated using flat priors. Trees were sampled every 1000 generations. The first 25% of saved trees were discarded as ‘burn-in’ samples. Stationarity was confirmed both by the standard deviation of split frequencies being below 0.01, and by comparing the two tree files using Tracer (Rambaut & Drummond 2007) and AWTY (Nylander *et al.* 2008).

## Results

The concatenated tree using all genes, with seven data partitions (codon positions for each gene plus tRNAs) had a likelihood of  $-\ln 42164.83$ . An SH test in RAXML that compared the best tree with a monophyly constraint for the genus *Rhacodactylus* was significantly different from the optimal tree at  $p < 0.05$ . The difference in likelihoods was  $-\ln 44.26$ , exceeding the standard deviation of the RELL bootstrapped trees by greater than a factor of 2. There were 1034 variable and 882 parsimony-informative characters for the ND2 analysis (henceforth referring to ND2 plus the five flanking tRNAs) and 1440 variable and 1122 parsimony informative characters in the combined ND2 and RAG1 analysis.

All analyses (ND2 only, RAG1, ND2 + RAG1; MP, ML and BI) found strong support for the monophyly of the New Caledonian diplodactylids as a group (Figs. 1–2). RAG1 only analyses (not shown) yielded no significant support for most internal nodes and not all species were recovered with support. All other analyses, however, retrieved monophyletic *Eurydactylodes* Wermuth, 1965 and *Dierogekko* Bauer, Jackman, Sadlier & Whitaker, 2006 with strong support, the latter as sister to the monotypic *Oedodera* Bauer, Jackman, Sadlier & Whitaker, 2006, although only with strong support in the Bayesian analyses. *Bavayia madjo* Bauer, Jones & Sadlier, 2000 was recovered as the sister to *Rhacodactylus* sensu lato (exclusive of the species assigned to *Correlophus*—see below)

and *Eurydactyloides* + all remaining *Bavayia* Roux, 1913 (Fig. 1, as *Paniegekko madjo*). As such, strong support for a monophyletic *Bavayia* was only obtained if *B. madjo* was excluded. Remaining *Bavayia* were strongly supported in the Bayesian analyses (pP = 0.98), but only weakly so under likelihood (69% bootstrap for combined tree, 53% for ND2 only). Within *Bavayia* the morphologically well-defined *B. cyclura*, *B. sauvagii*, and *B. ornata/septuiclavis* groups were retrieved with varying levels of support. None of the analyses found a monophyletic *Rhacodactylus*. In all cases *Eurydactyloides* was embedded inside part of *Rhacodactylus* as the sister to *R. chahoua*. This relationship has posterior probabilities of  $\geq 0.98$  in the Bayesian analyses and bootstrap support of  $\geq 96\%$  in the ML analyses. In addition, the strongly-supported sister species pair of *R. ciliatus* and *R. sarasinorum* were consistently outside the clade that included their remaining congeners plus *Eurydactyloides* as sister to a clade comprising all New Caledonian taxa exclusive of *Oedodera* + *Dierogecko*, although with low support. One of the only conflicts between the ND2 and combined trees is seen in *Rhacodactylus*. In the ND2 tree *Rhacodactylus trachyrhynchus* (including *R. trachycephalus*) is the sister of *R. auriculatus*, but with poor support, and was sister to *R. leachianus* in the combined analysis, again with poor support. In the combined tree *R. auriculatus* was sister to (*R. trachyrhynchus* + *R. leachianus*) + (*Eurydactyloides* + *R. chahoua*). This pattern received strong support in the Bayesian analysis, but only moderate bootstrap support under ML and MP. No higher order groupings of *Rhacodactylus* species receive support except that the clade including *Eurydactyloides* plus all *Rhacodactylus* exclusive of *R. ciliatus* and *R. sarasinorum* is strongly supported under BI (pP = 0.96–1.00) and weakly so in the likelihood analyses (66–68% bootstraps).

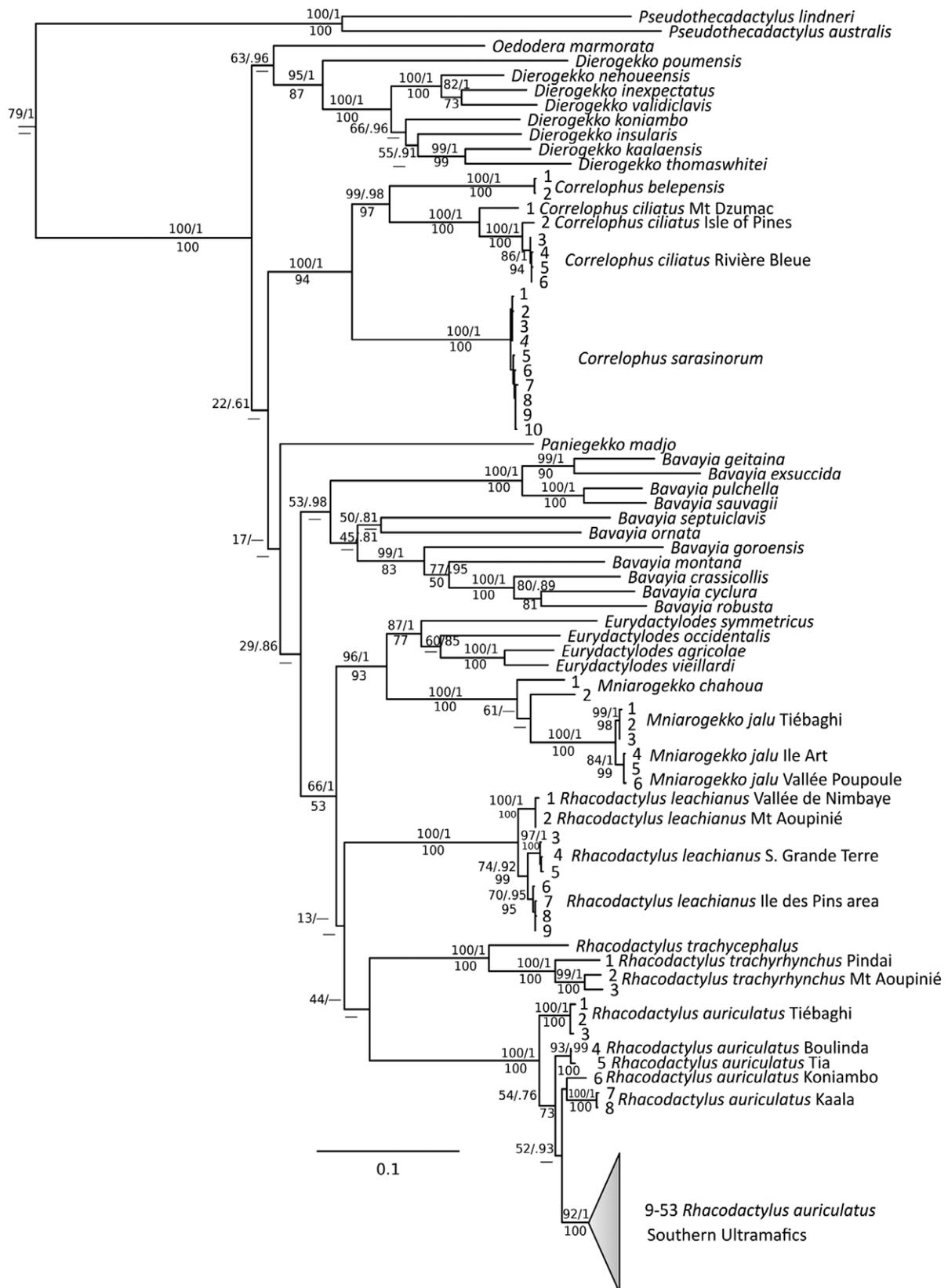
All *Rhacodactylus* species are monophyletic and levels of intraspecific variation are generally much lower than interspecific differences. There is virtually no variation across the 10 specimens of *R. sarasinorum* sampled and divergences across *R. leachianus* samples are also relatively small. *Rhacodactylus auriculatus* exhibits near uniformity across its continuous range in southern New Caledonia, whereas northern populations are modestly divergent from one another. Deeper divergences characterize *R. trachyrhynchus*, *R. chahoua*, and especially *R. ciliatus*.

**Systematics.** Our dataset is dominated by the mitochondrial ND2 gene. Although RAG1 did not recover well-supported relationships within *Rhacodactylus* or other New Caledonian genera, its combination with ND2 (Fig. 2) resulted in topologies that differed somewhat from the ND2 tree (Fig. 1) only with respect to the placement of *R. auriculatus* and several species of *Dierogecko*. We believe that the relatively rapid diversification of the New Caledonian gecko radiation has not been captured by the slowly evolving nuclear locus. Further, whereas the ND2 topology is strongly supported, the conflicting RAG1 topology is not. We therefore accept the ND2 topology as the current best estimation of relationships and reevaluate the taxonomy of *Rhacodactylus* accordingly. Interestingly, however, some relationships in the combined tree, for example, the monophyly of both *Bavayia* (exclusive of *B. madjo*) and *Eurydactyloides*, receive substantially higher ML bootstrap support than in the ND2 tree only. The effect of additional nuclear genes on clade support has been considered by Skipwith (2011).

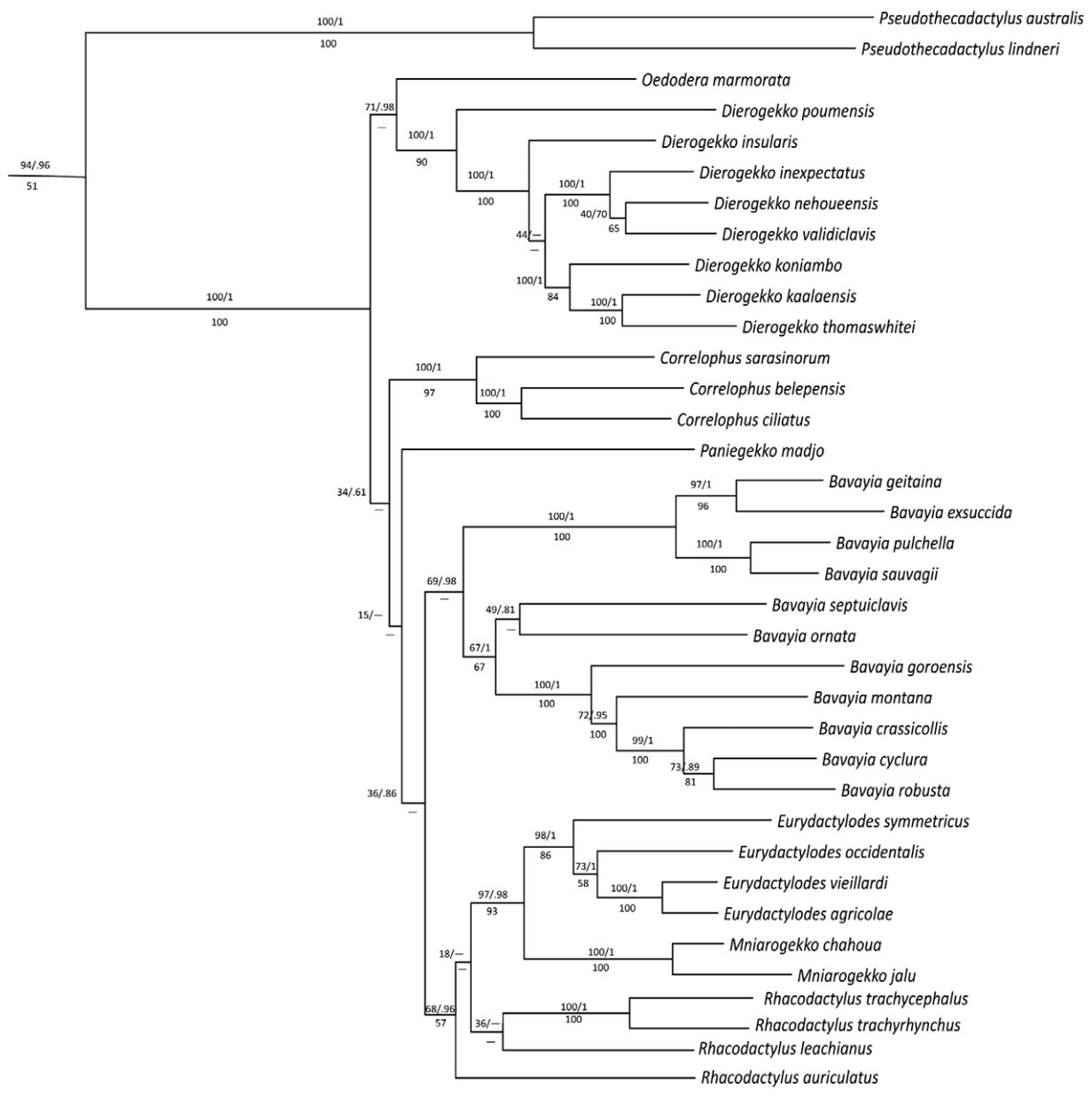
**Taxonomic Implications at the Generic Level.** We reject the monophyly of *Rhacodactylus* both on the grounds that it is made paraphyletic by its inclusion of *Eurydactyloides*, and because of the apparent polyphyletic origin of the six recognized species.

The type species of *Rhacodactylus* Fitzinger, 1843 by original designation is *Ascalabotes leachianus* Cuvier, 1829 and the name is therefore linked to this species. That *R. ciliatus* and *R. sarasinorum* are sister taxa is unambiguous and consistent with the findings of Vences *et al.* (2001) and Bauer *et al.* (2004). That this clade is also not part of *Rhacodactylus* *sensu stricto* is likewise strongly supported by our analyses. *Correlophus* Guichenot, 1866, with *C. ciliatus* Guichenot, 1866 as its type species by monotypy, is the available generic name for this clade which we here resurrect from the synonymy of *Rhacodactylus*.

The sister relationship between *Eurydactyloides* and *Rhacodactylus chahoua* has been previously noted (Bauer *et al.* 2009), although the taxonomic implications of this finding have not yet been addressed. To maintain the monophyly of *Rhacodactylus* (exclusive of *Correlophus*) would require that *Eurydactyloides* be synonymized with it. Alternatively, if *Eurydactyloides* were to be retained this would necessitate the recognition of one or more additional genera for the giant geckos, depending upon the topology of the reference phylogeny. Either solution requires some degree of disruption to the existing usage of names, which has been relatively stable for more than a century (Boulenger 1883; Roux 1913). Although we are opposed to the arbitrary proliferation of generic names, particularly when monotypic taxa are involved, in this instance we believe that the maintenance of *Eurydactyloides* as a separate genus is warranted for this clade of four species that is defined by an extensive suite of morphological



**FIGURE 1.** Maximum likelihood tree based on the mitochondrial ND2 gene and flanking tRNAs showing relationships among species of New Caledonian diplodactylids and their immediate sister-group, the Australian genus *Pseudothecadactylus*. Values subtending branches are maximum likelihood/ Bayesian posterior probabilities above the line and maximum parsimony bootstrap values below the line. Dashes for posterior probabilities indicate no support for the maximum likelihood topology whereas dashes for maximum parsimony bootstraps indicates values < 50%. Support values are not shown for conspecific relationships where samples differ by three or fewer bases. In the case of *Rhacodactylus auriculatus* southern ultramafic block samples are cumulatively represented as a triangle.



**FIGURE 2.** Maximum likelihood tree based on the combined mitochondrial (ND2 and flanking tRNAs) and nuclear genes (RAG1) showing relationships among species of New Caledonian diplodactylids and their immediate sister-group, the Australian genus *Pseudothecadactylus*. The tree has been pruned to show only one exemplar for each taxon. Both intra- and interspecific patterns of relationship are nearly identical to those supported by ND2 only (Fig. 1). Only within *Dierogekko* and *Rhacodactylus sensu stricto* are alternative patterns hypothesized (see text). Values subtending branches are maximum likelihood/ Bayesian posterior probabilities above the line and maximum parsimony bootstrap values below the line. Dashes for posterior probabilities indicate no support for the maximum likelihood topology whereas dashes for maximum parsimony bootstraps indicates values < 50%.

apomorphies. We choose this option to reflect the very obvious morphological and behavioral differences between *R. chahoua* and *Eurydactylodes* and also to maintain the historical continuity of name usage. While neither has an extensive history of use (Bauer 1985; Bauer & Henle 1994; Bauer *et al.* 2009), both have been employed consistently over a long period of time. *Eurydactylodes* are small (maximum SVL 60.3 mm), slow-moving, laterally-compressed geckos, with a tail-squirting defensive mechanism (Böhme & Sering 1997) and greatly

enlarged head scales. They have enlarged extracranial endolymphatic sacs (Bauer 1989), partly calcified egg shells (Bauer & Sadlier 2000), and are at least partly diurnal. In contrast, *R. chahoua* are large-bodied (Bauer 1985), nocturnal, and retain the plesiomorphic New Caledonian diplodactylid condition with respect to scale size, endolymphatic system, and tail morphology. Further, mitochondrial sequence divergence between *R. chahoua* and *Eurydactylodes* spp. averages 14.3%, as deeply divergent as between any two of the monophyletic genera of New Caledonian diplodactylids. *Rhacodactylus chahoua* was formerly confused with *R. trachyrhynchus* (Sauvage 1879; Boulenger 1879; Bocage 1881; see Bauer 1985) and was briefly allocated, along with it, to the genus *Chameleonurus* but this name is associated with the latter species. Thus, there are no available generic names for *R. chahoua* and a new name is proposed below.

Under the tree topology obtained from the maximum likelihood analysis of the mitochondrial data (Fig. 1), *Rhacodactylus leachianus*, *R. trachyrhynchus* and *R. auriculatus* form a monophyletic group exclusive of *R. chahoua* plus *Eurydactylodes*, albeit without bootstrap support. In this instance only the allocation of a new name to *R. chahoua* would be required to maintain monophyletic genera. However, as noted above, each of our analyses retrieves a different topology and most have no support for patterns of relationship within the *Rhacodactylus* (exclusive of *Correlophus*) + *Eurydactylodes* clade except for the sister relationship of the latter genus to *R. chahoua*. Consistent with this uncertainty, we adopt the temporary solution of retaining the remaining taxa within *Rhacodactylus* Fitzinger, 1843. *Ceratolophus* Bocage, 1873 and *Chameleonurus* Boulenger, 1878 are synonyms applicable to *R. auriculatus* and *R. trachyrhynchus* (and *R. trachycephalus*, see below), respectively, and are available should future resolution of relationships warrant the further fragmentation of the three species here retained in a redefined *Rhacodactylus*.

In addition to taxonomic implications for *Rhacodactylus* sensu lato, our phylogenetic results strongly support the non-monophyly of *Bavayia*. Specifically, the high-elevation endemic *B. madjo* receives no support as part of the clade including all other members of the genus. Intrageneric relationships within *Bavayia* sensu stricto will be addressed elsewhere, but we take this opportunity to erect a new genus to accommodate this highly-divergent species. Details of the new generic arrangements implemented here are presented below. We recognize eight genera of diplodactylid geckos in New Caledonia (Fig. 3), each strictly endemic to the territory.

**A New Classification of New Caledonian Diplodactylid Geckos.** Based on the arguments above, we recognize eight genera of New Caledonian diplodactylid geckos. Weak support for some groupings suggests that further adjustments may be necessary when more data are available, but we believe that the following allocation of species to genera provides the best reflection of our current knowledge of relationships within the group while also accommodating, as far as is possible, the historical application of names.

## ***Oedodera* Bauer, Jackman, Sadlier & Whitaker, 2006**

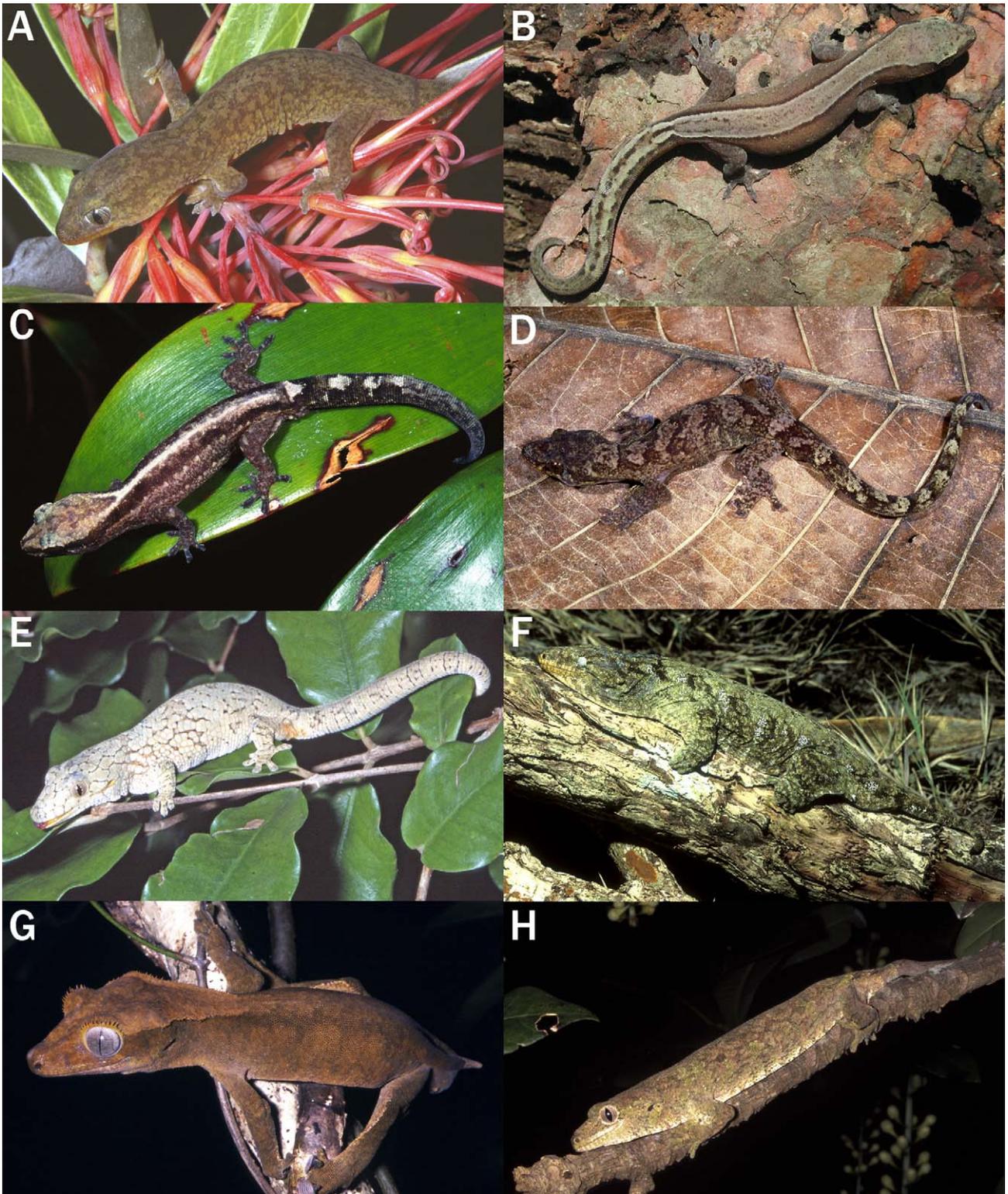
**Content.** *Oedodera marmorata* Bauer, Jackman, Sadlier & Whitaker, 2006 (Fig. 3A)

Type species: *Oedodera marmorata* Bauer, Jackman, Sadlier & Whitaker, 2006 by original designation.

**Diagnosis.** *Oedodera* may be distinguished from all other New Caledonian diplodactylid genera by the following combination of character states: body size small (to 61 mm SVL); head large, neck distinctly swollen, nearly as wide as the widest part of head; tail to 93% of SVL; dorsal scalation granular, homogeneous; body without extensive skin webs or flaps; expanded, undivided subdigital lamellae under all toes; reduced claw of digit I of manus and pes situated between an asymmetrical pair of apical scancers; digit I of pes only with a small rounded scale on medial side in gap between subdigital lamellae and apical scancers; medial apical scensor present on digit II of one or more feet (condition variable); precloacal pores in two or three short rows (fewer than 20 pores in total) not extending onto thighs, females with precloacal slits or pits without secretory material; dorsal pattern of marbled or reticulated brown; venter distinctly yellowish.

**Distribution.** *Oedodera* is limited to maquis habitat on ultramafic substrates in the far northwest of New Caledonia.

**Remarks.** Since the description of *O. marmorata*, from Paagoumène, additional populations of *Oedodera* have been discovered and their taxonomic status is currently under review.



**FIGURE 3.** Representatives of each of the eight genera of endemic New Caledonian diplodactylid geckos. A. *Oedodera marmorata*. B. *Dierogekko nehoueensis*. C. *Bavayia pulchella*. D. *Paniegekko madjo*. E. *Eurydactylodes occidentalis*. F. *Rhacodactylus leachianus*. G. *Correlophus belepensis* **sp. nov.** H. *Mniarogekko jalu* **sp. nov.** Photos A, E, G–H by A.H. Whitaker, photo B by A.M. Bauer, photos C–D by R.A. Sadlier. Photo F courtesy of Mark O’Shea.

## ***Dierogecko* Bauer, Jackman, Sadlier & Whitaker, 2006**

**Content.** *Dierogecko validiclavis* (Sadlier, 1989), *D. inexpectatus* Bauer, Jackman, Sadlier & Whitaker, 2006, *D. insularis* Bauer, Jackman, Sadlier & Whitaker, 2006, *D. kaalaensis* Bauer, Jackman, Sadlier & Whitaker, 2006, *D. koniambo* Bauer, Jackman, Sadlier & Whitaker, 2006, *D. nehoueensis* Bauer, Jackman, Sadlier & Whitaker, 2006 (Fig. 3B), *D. poumensis* Bauer, Jackman, Sadlier & Whitaker, 2006, *D. thomaswhitei* Bauer, Jackman, Sadlier & Whitaker, 2006.

**Type species.** *Bavayia validiclavis* Sadlier, 1989 by original designation.

**Diagnosis.** *Dierogecko* may be distinguished from all other New Caledonian diplodactylid geckos by the following combination of character states: body size very small (< 46 mm SVL); head small; tail 92–120% of SVL; dorsal scalation granular, homogeneous; body without extensive skin webs or flaps; expanded subdigital lamellae under all toes; lamellae under penultimate phalanx of digits II–V of manus and pes paired or single; claw of digit I of manus and pes in a groove in the apical lamella between a larger medial scansor and a smaller lateral scansor; precloacal pores in one or two rows in males (10–20 pores in total), not extending onto thighs; dorsal pattern of longitudinal lines or series of spots or patternless, never with transverse markings; venter usually cream to light brown, sometimes pale yellow.

**Distribution.** *Dierogecko* is restricted to northern New Caledonia, with populations extending up the west coast from the Massif de Koniambo to Poum and on the Panié massif (Mt. Mandjélia and Mt. Panié) on the east coast. It is also known from the northern islands of Île Yandé and Île Baaba, and on Île Art and Île Pott in the Îles Belep. It is likely that its distribution is more continuous across this region than existing data show.

**Remarks.** See Bauer and Sadlier (2000) and Bauer *et al.* (2006b) for detailed information on members of this genus. Additional field work in northern New Caledonia has revealed a new species of *Dierogecko* on Île Baaba and hitherto unexpected genetic variation in *D. koniambo* (Skipwith *et al.* submitted).

## ***Bavayia* Roux, 1913**

**Content.** *Bavayia cyclura* (Günther, 1872), *B. sauvagii* (Boulenger, 1883), *B. montana* Roux, 1913, *B. crassicollis* Roux, 1913, *B. ornata* Roux, 1913, *B. septuiclavis* Sadlier, 1989, *B. exsuccida* Bauer, Whitaker & Sadlier, 1998, *B. pulchella* Bauer, Whitaker & Sadlier, 1998 (Fig. 3C), *B. geitaina* Wright, Bauer & Sadlier, 2000, *B. robusta* Wright, Bauer & Sadlier, 2000, *B. goroensis* Bauer, Jackman, Sadlier, Shea & Whitaker, 2008, *Bavayia nubila* Bauer, Sadlier, Jackman & Shea, 2012.

**Type species.** *Peripia cyclura* Günther, 1872 by original designation.

**Diagnosis.** *Bavayia* may be distinguished from all other New Caledonian diplodactylid geckos by the following combination of character states: body size small to moderate (47–86 mm SVL); head small to large; tail 85–112% of SVL; dorsal scalation granular, homogeneous; body without extensive skin webs or flaps; expanded subdigital lamellae under all toes; lamellae under digits II–V divided, at least distally; claw of digit I of manus and pes in a groove in the apical lamella between a larger medial scansor and a smaller lateral scansor or lateral to an unpaired apical scansor; precloacal pores in one or two rows in males, not extending onto thighs (7–40 pores in total); dorsal color pattern brown usually with chevrons or transverse bands or blotches (except in *B. pulchella* and *B. septuiclavis*, in which longitudinal stripes or series of small dots may be present or which may be virtually patternless); venter cream, grayish, or yellow.

**Distribution.** *Bavayia* is the most widespread genus of New Caledonian diplodactylids. On the Grand Terre it occurs island-wide. It is also present on the Îles Belep, the Île des Pins, the Loyalty Islands, and probably all smaller satellite islands.

**Remarks.** See Bauer and Henle (1994) and Bauer and Sadlier (2000) for detailed information on members of this genus. Many additional cryptic taxa from throughout the Grande Terre have been identified on genetic grounds and await description (Jackman & Bauer 2006).

## ***Paniegekko* Bauer, Jackman, Sadlier & Whitaker gen. nov.**

**Content.** *Paniegekko madjo* (Bauer, Jones & Sadlier, 2000) (Fig. 3D)

**Type species.** *Bavayia madjo* Bauer, Jones & Sadlier, 2000, here designated.

**Etymology.** The generic name is derived from the Panié massif, the dominant landform of northeastern New Caledonia, and *gekko*, from the Malay ‘gekoq’, onomatopoeia of the call of the species *Gekko gekko* and the common name to all limbed gekkotans. A Sri Lankan origin for the word gekko, derived from the Sinhalese word ‘gego’, is also possible (de Silva & Bauer 2008). The name is masculine and should be pronounced “Pa-nē-ā-gekko.” The two known localities for this monotypic genus are Mt. Ignambi and Mt. Panié, both part of the Panié massif.

**Definition and Diagnosis.** *Paniegekko* may be distinguished from all other New Caledonian diplodactylid geckos by the following combination of character states: body size moderate (to 75mm SVL), head large, tail slender and elongate (> 110% SVL); dorsal scalation granular, homogeneous; body without extensive skin webs or flaps; expanded subdigital lamellae under all toes; subdigital lamellae of digits II–V of manus and pes unpaired basally and divided distally; claw of digit I of manus and pes positioned lateral to a single, undivided apical lamella; precloacal pores in two or more rows in males, longest row extending well onto thighs (50 or more pores total); dorsal coloration pattern brown with transverse chevrons; venter dull grayish, never yellow.

**Distribution.** *Paniegekko* is known only from Mt. Ignambi and Mt. Panié in northeastern New Caledonia.

**Remarks.** See Bauer and Sadlier (2000) for more information on *P. madjo*. Erection of a new genus for *Bavayia madjo* was necessitated to maintain the monophyly of *Bavayia* (see above).

## ***Eurydactylodes* Wermuth, 1965**

**Content.** *Eurydactylodes vieillardii* (Bavay, 1869), *E. symmetricus* (Andersson, 1908), *E. agricolae* Henkel & Böhme, 2001, *E. occidentalis*, Bauer, Jackman, Sadlier & Whitaker, 2009 (Fig. 3E).

**Type species.** *Platydactylus vieillardii* Bavay, 1869 by monotypy [as type of *Eurydactylus* Sauvage, 1878; this name was preoccupied by *Eurydactylus* Laferté, 1851 = Coleoptera]

**Diagnosis.** *Eurydactylodes* is distinguished from all other New Caledonian diplodactylid gekkotans by the following combination of characters: body size small (to 60.3 mm SVL); neural spines of trunk vertebrae elongate, body laterally compressed, six or seven inscriptional ribs, dorsal body scalation consists of enlarged, smooth, flattened scales; dorsal head scales enlarged to greatly enlarged; a postlabial slit present, confluent or not with subauricular groove; endolymphatic sacs expanded extracranially; margins of jaws and limbs with folds of skin; subdigital lamellae undivided or with irregular divisions; claw of digit I of manus and pes lies between a pair of separate terminal subdigital scansors; precloacal pores in males in 3–5 rows sometimes extending onto base of thighs (50–68 pores in total); original tail (100–115% of SVL) with distal adhesive subcaudal lamellae and possessing caudal glands and a “tail-squirting” mechanism; tongue and mouth lining yellow to orange; dorsal color pattern grayish, cream, tan, or beige with darker transverse bands or markings; venter white.

**Distribution.** *Eurydactylodes* has been recorded from the Îles Belep (Île Art and Île Pott only), Île Yandé, the Grande Terre and Île des Pins, but has not been found on the Loyalty Islands or any smaller satellite islands.

**Remarks.** See Bauer and Henle (1994); Bauer and Sadlier (2000), and Bauer *et al.* (2009) for additional details about this genus.

## ***Rhacodactylus* Fitzinger, 1843**

**Content.** *Rhacodactylus leachianus* (Cuvier, 1829) (Fig. 3F), *R. auriculatus* (Bavay, 1869), *R. trachyrhynchus* Bocage, 1873; *R. trachycephalus* (Boulenger, 1878).

**Type species.** *Ascalabotes leachianus* Cuvier, 1829 by original designation.

**Diagnosis.** *Rhacodactylus* may be distinguished from all other New Caledonian diplodactylid geckos by the following combination of character states: body large to very large (maximum 125–256 mm SVL); head large, skull usually ornamented with bumps, ridges or rugosities; tail variable across species, 30–100% of SVL; dorsal

scallation granular, homogeneous; extensive skin folds present or absent; expanded undivided subdigital lamellae under all toes; webbing between digits weakly to strongly developed; claw of digit I of manus and pes positioned lateral to a single, undivided apical lamella; precloacal pores in three to six rows (occasionally up to eight rows, but posteriormost one or two with only scattered pores) in males (49–130 pores in total), longest anterior rows extending on to base of thighs or not; dorsal color pattern highly variable both within and between species.

**Distribution.** *Rhacodactylus* spp. occur throughout most of the Grande Terre — as far north as the Dôme de Tiébaghi in the west and the Panié massif in the east — but they have not been recorded in the far north of Grande Terre and among its smaller satellite islands they have only been recorded on one (Île Némou). They are also present on the Île des Pins and its surrounding satellite islands but are absent from the Loyalty Islands.

**Remarks.** The four species here retained in a redefined *Rhacodactylus* represent three morphologically distinct units. Although we retrieve a monophyletic *Rhacodactylus* under maximum likelihood in the ND2 tree, the low level of support for this arrangement does not exclude the possibility that each of these units represents an independent lineage with closer affinities to other New Caledonian genera than to one another. Were this the case, the name *Rhacodactylus* is linked to *R. leachianus* and the names *Ceratolophus* Bocage, 1873 and *Chameleonurus* Boulenger, 1878 are available for *R. auriculatus* and the live-bearing forms, respectively. See below for a discussion of the revalidation of *R. trachycephalus*.

### ***Correlophus* Guichenot, 1866**

**Content.** *Correlophus ciliatus* Guichenot, 1866, *C. sarasinorum* (Roux, 1913), *C. belepensis* **sp. nov.** Bauer, Whitaker, Sadlier & Jackman, 2012 (Fig. 3G; see below for description).

**Type species.** *Correlophus ciliatus* Guichenot, 1866 by monotypy

**Diagnosis.** *Correlophus* may be distinguished from all other New Caledonian diplodactylid geckos by the following combination of character states: body large (to 135 mm SVL); head large; tail approximately 80–92% of SVL; dorsal scallation granular, homogeneous or mostly so; extensive skin folds lacking, but small ventrolateral folds and folds on the posterior margins of the limbs present in some species; a pair of crests comprised of enlarged triangular scales extending from behind orbits and onto body dorsum, or pale markings delimiting the equivalent area; expanded undivided subdigital lamellae under all toes; webbing between digits weakly to moderately developed; claw of digit I of manus and pes positioned lateral to a single, undivided apical lamella; precloacal pores in two to three rows in males (40–60 pores in total), extending on to basal 40% of thighs; dorsal color pattern brown, olive, yellowish, reddish, or orangey usually with or without contrasting markings on the crown, vertebral area or on flanks; venter beige to color of dorsum.

**Distribution.** *Correlophus* appears to have a disjunct distribution, occurring on the Île des Pins, the southern Grande Terre as far north as Canala, and on the Îles Belep.

**Remarks.** See below for the description of a new species of *Correlophus*.

### ***Mniarogekko* Bauer, Whitaker, Sadlier & Jackman gen. nov.**

**Content.** *Mniarogekko chahoua* (Bavay 1869), *M. jalu* **sp. nov.** Bauer, Whitaker, Sadlier & Jackman, 2012 (Fig. 3H; see below for description).

**Type species.** *Platydactylus chahoua* Bavay, 1869, here designated.

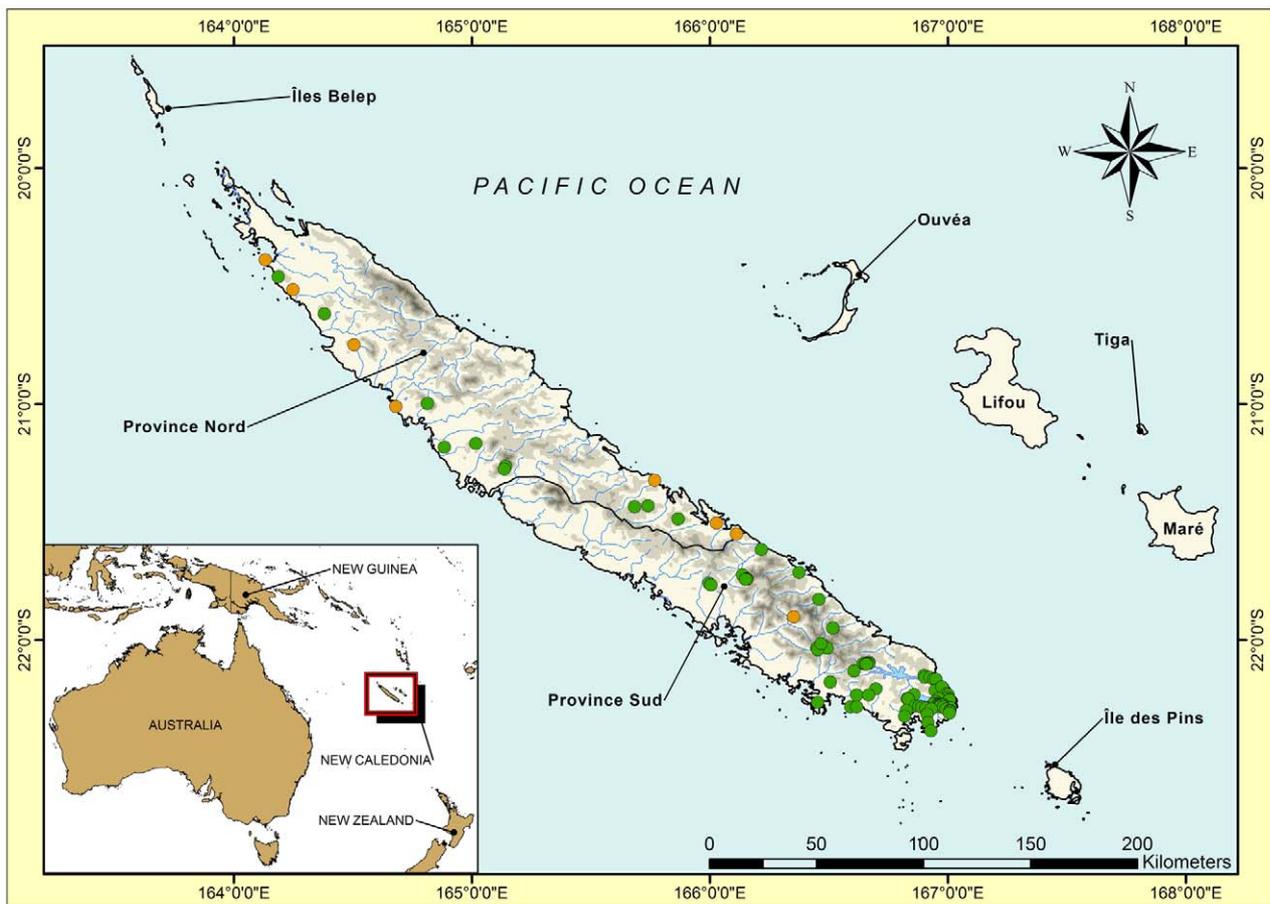
**Etymology.** The generic name is derived from the Greek word *mniaros*, meaning mossy and *gekko*, from the Malay ‘gekoq’, onomatopoeia of the call of the species *Gekko gekko* and the common name to all limbed gekkotans. A Sri Lankan origin for the word gekko, derived from the Sinhalese word ‘gego’, is also possible (de Silva & Bauer, 2008). The name is masculine and should be pronounced “Nē-aro-gekko.” It refers to the mossy or lichenous markings that are common on members of this genus. The vernacular names “New Caledonian mossy gekko” and “Mossy prehensile-tailed gekko” are in wide use in the herpetocultural literature for *M. chahoua* (de Vosjoli *et al.* 2003).

**Definition and Diagnosis.** *Mniarogekko* may be distinguished from all other New Caledonian diplodactylid geckos by the following combination of character states: body large (to 147 mm SVL); head moderately-sized; tail

approximately equal to SVL; dorsal scalation granular, homogeneous; loose folds of skin present on margins of mandible and along ventrolateral border of body; expanded undivided subdigital lamellae under all toes; webbing between digits relatively extensive; claw of digit I of manus and pes positioned lateral to a single, undivided apical lamella; precloacal pores in three or four rows in males, anterior two rows extending onto base of thighs (70–120 pores in total); dorsal color pattern highly variable but consisting of a gray, olive, brown, reddish or orangey background usually with dark middorsal blotches and/or transverse markings, with one or more patches of ashy to lichenous green patches; venter cream to greenish.

**Distribution.** *Mniarogekko* occurs broadly on the Grande Terre. Seipp and Henkel (2000, 2011) believed that *M. chahoua* occurred island-wide, but the number of verified localities is limited and there may be large gaps (Langner 2009). Nearly all known locality records from the Grande Terre are from low elevation valleys. The genus also is present on the Îles Belep and has been recorded from unstated localities on the Île des Pins (Seipp & Klemmer 1994; Seipp & Obst 1994; de Vosjoli 1995; de Vosjoli & Fast 1995; Seipp & Henkel 2000, 2011).

**Remarks.** See below for the description of a new species of *Mniarogekko*.



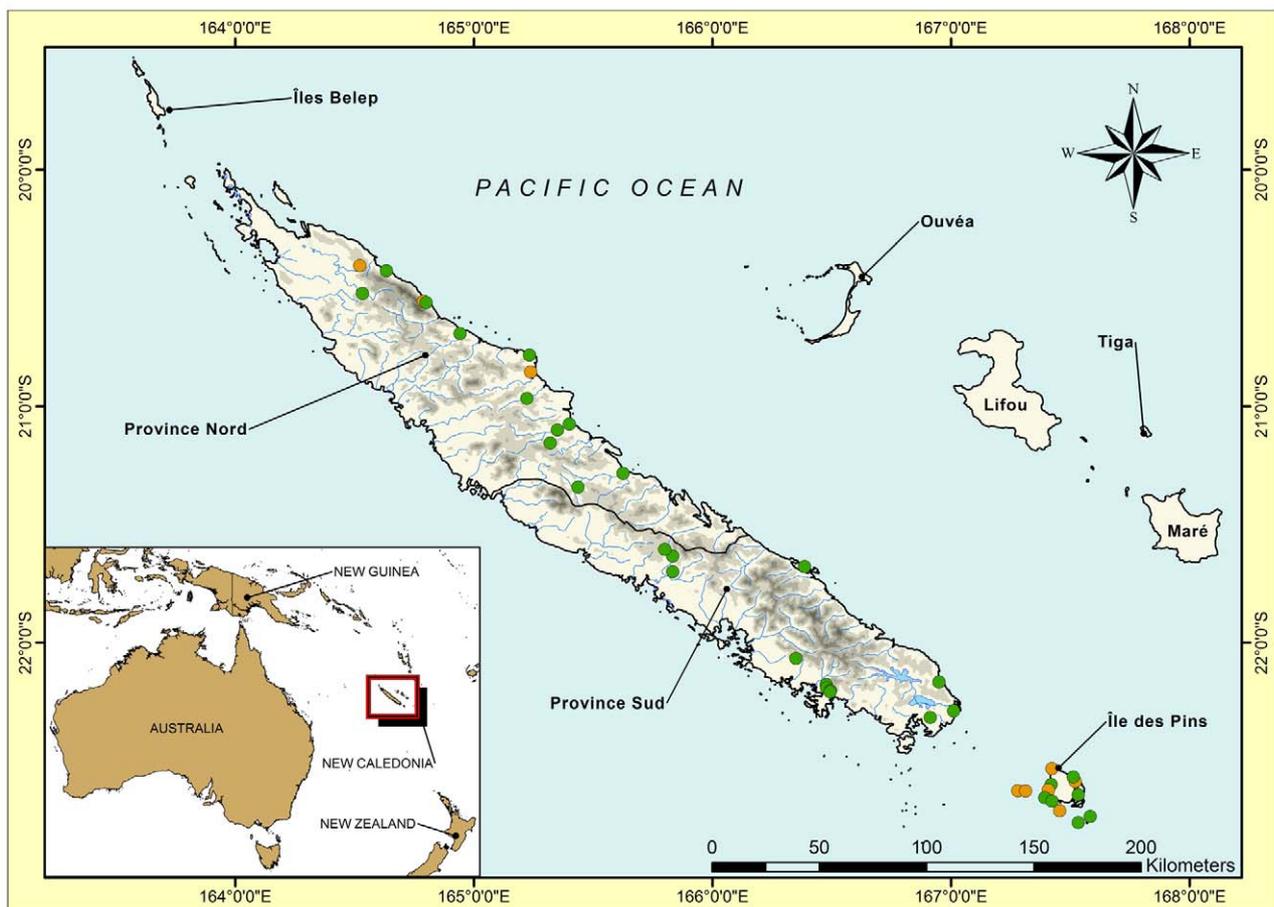
**FIGURE 4.** Distribution map of *Rhacodactylus auriculatus* (circles). Green symbols represent vouchered records, orange symbols represent unvouchered sight or literature records. See Appendix for a list of localities mapped.

## Intraspecific variation in New Caledonian Giant Geckos

### *Rhacodactylus*

*Rhacodactylus auriculatus*—Variation is limited in *R. auriculatus* (Figs. 1–2). Until recently this species was believed to be restricted to the southern ultramafic block of the Grande Terre (Bauer & Sadlier 2000, 2001). There is little divergence or substructure within the clade from this region. This is consistent with Bauer’s (1990)

observation that *R. auriculatus* is polymorphic in color throughout this range and shows no geographically-related trends in character variation, and with the lack of allozyme variation reported by Good *et al.* (1997). However, extensive field surveys in the northern ultramafic ranges of the Grande Terre undertaken by the authors beginning in 2001, have revealed that *R. auriculatus* also occurs as far north as Dôme de Tiébaghi in the west and Poro in the east (Whitaker *et al.* 2004; Bauer *et al.* 2006a, b; Fig. 4). Our samples included specimens from the Dôme de Tiébaghi, Mt. Kaala, Massif de Koniambo, Plateau de Tia, Massif de Kopéto and Massif du Boulinda. Samples from the southernmost of these localities (Tia, Boulinda) are nearly genetically identical to one another, but each of the other localities, representing three isolated ultramafic blocks, are divergent, albeit at a low level (3.1–4.1%). The northernmost locality of Dôme de Tiébaghi is the most deeply divergent lineage. However, this divergence is less than between well-diagnosed species of *Dierogekko* or other giant geckos and we interpret the pattern seen as the result of isolation by distance within a lineage now known to have an almost island-wide distribution on ultramafic surfaces. The lack of variation within the southern ultramafic block or the Boulinda-Kopéto block probably reflects the continuity of gene flow between largely continuous blocks of maquis habitat or possibly recent rapid expansion. Unlike its congeners, *R. auriculatus* readily moves on the ground (Bauer and Vindum, 1990) and occurs in maquis vegetation and at least on the periphery of humid forest habitat (Snyder *et al.* 2010). Given that the northern populations of *R. auriculatus* escaped detection for nearly 150 years, it is possible that the species is even more widely distributed on ultramafic surfaces than now indicated.



**FIGURE 5.** Distribution map of *Rhacodactylus leachianus* (circles). Green symbols represent vouchered records, orange symbols represent unvouchered sight or literature records. See Appendix for a list of localities mapped.

*Rhacodactylus leachianus*—Morphological variation in *Rhacodactylus leachianus*, at least with respect to size, body proportions, and color pattern, has been remarked upon by numerous authors (e.g., Henkel 1991, 1993; Seipp & Obst 1994; Seipp & Henkel 2000, 2011; de Vosjoli *et al.* 2003; Cemelli 2009; Schönecker & Schönecker 2009b). In particular, *R. leachianus* from the offshore islands surrounding the Île des Pins have been recognized as *R. l. henkeli* Seipp and Obst, 2004. Geckos from these populations are generally characterized by smaller size,

stouter body, shorter snouts and tails, lower scale counts, and heavier patterning than most individuals from the Grande Terre. They have also been regarded as being more diurnal and less wary than individuals from the Grande Terre (Seipp & Obst 1994; de Vosjoli 1995). Further, many “varieties” or “morphs” from different southern islands have been identified and are marketed as discrete entities in the pet trade (de Vosjoli *et al.* 2003; Cemelli, 2009). Good *et al.* (1997) reviewed the evidence for the recognition of *R. l. henkeli* and concluded that the scale counts and color patterns seen in the insular forms fell within the range of variation of the nominate form. They further argued that features such as smaller size and reduced wariness might be expected on islands, where resources are limited and predators absent. Lower scale counts may be a direct consequence of smaller body size (Hecht 1952).

In fact, the level of genetic differentiation between populations of *R. leachianus* on the Grande Terre may be greater than that observed between populations on the southern islets and the main island. Vences *et al.* (2001) found no variation between specimens from four islands in the Île des Pins group and only a single base pair difference between these and a specimen from Nouméa in the southern Grande Terre. They did, however, find 18–19 base-pair differences between these southern forms and a specimen from Houaïlou on the central east coast. Our sampling within *R. leachianus*, which occurs throughout much of New Caledonia (Fig. 5), was limited (Table 1), but included specimens from two southern islands (Môrô and Bayonnaise), a far southern mainland locality (Kwa Néie), and two central localities (Mt. Aoupinié and Vallée de Nimbaye). The northernmost localities sampled were largely invariant and were sister to the southern ones, including the islands (Fig. 1), but the level of divergence was minimal, about half of that between northern and southern *R. auriculatus*, and the divergence between the southern mainland and islands was only 1.4%.

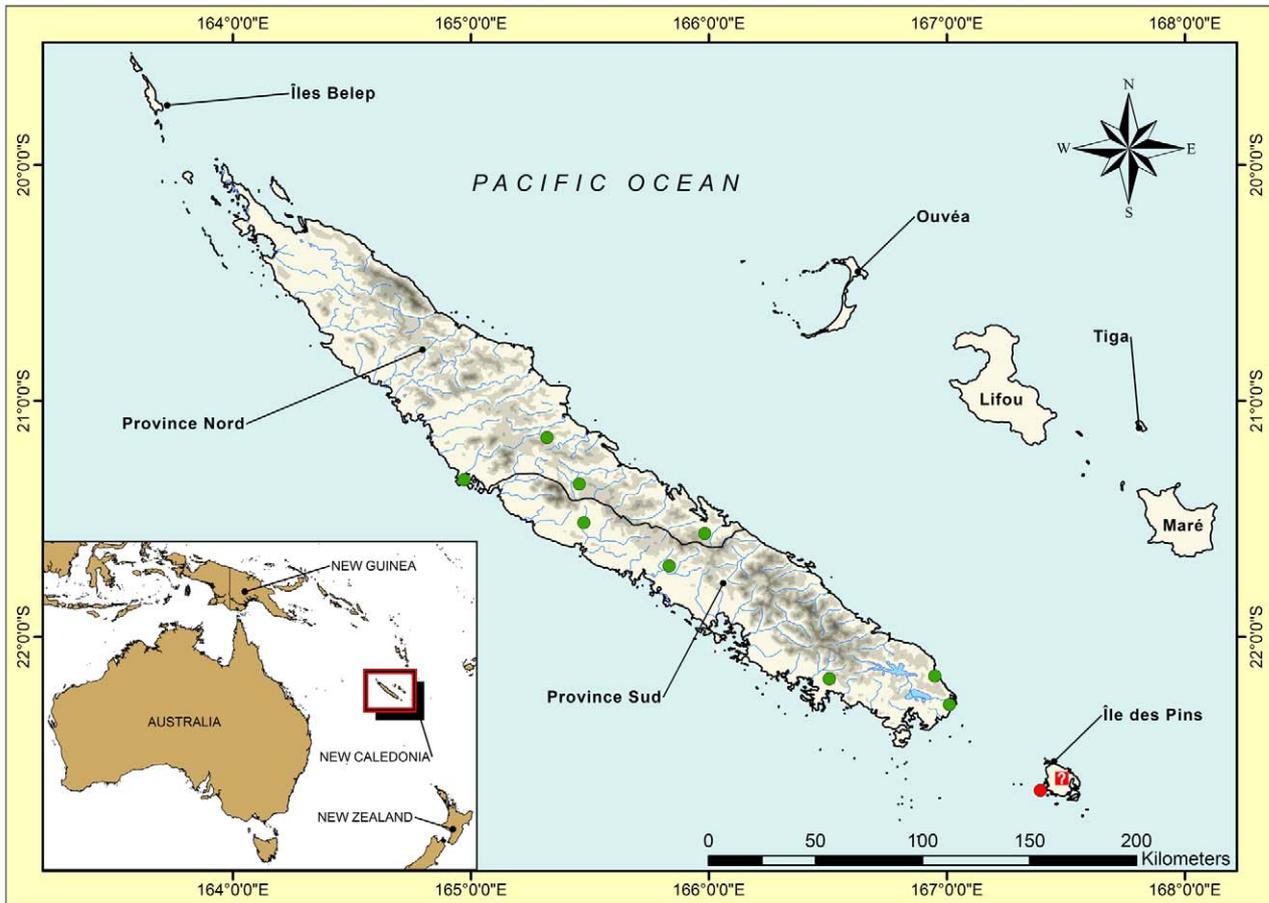
Although we do not doubt the observed phenotypic differences between the mainland and insular forms, we believe that most of these differences represent either phenotypically plastic traits or traits that have become fixed in very recent times. Indeed sea level minima of 100 m or more would have connected the Grande Terre to the Île des Pins as recently as 16,000–20,000 years ago (Holloway 1979; Balouet & Olson 1989), although the presence or extent of suitable habitat on the land exposed by lower sea levels is unknown. Further, cyclones in the region are known to overwash and denude some of the small islands upon which *R. leachianus* lives (Geneva 2008). This suggests that existing populations may reflect not simply lizards isolated by rising sea levels, but the result of many recolonizations from either the Île des Pins proper or the southern Grande Terre. We therefore echo Good *et al.* (1997) in regarding “*henkeli*” as a morph of typical *R. leachianus* peculiar to the southern islets, rather than as a valid taxon.

The status of *R. aubrianus* Bocage, 1873, which has been recognized subspecifically by some authors (Roux 1913; Kluge 1967) cannot be evaluated. The syntypes of this form were destroyed by fire in 1978 (Almaça & Neves 1987) and are without specific locality. Putatively diagnostic features of snout scalation given by Bocage (1873) as diagnostic, in fact, also occur in some typical *R. leachianus*. Thus, we also regard this form as strictly synonymous with *R. leachianus*, which is therefore, monotypic. Seipp and Henkel (2011) suggested that *R. leachianus* “dark morph” was distinct in coloration and biology from the typical form and that these two occurred in sympatry in some areas.

*Rhacodactylus trachyrhynchus* and *R. trachycephalus* — Boulenger (1878) described *Chameleonurus trachycephalus* from the Île des Pins, but later synonymized his new genus and species with *Rhacodactylus trachyrhynchus* (Boulenger 1883). The name remained largely unused for more than a century, until used in a subspecific context by Seipp and Obst (1994), Kluge (2001), and Seipp and Henkel (2000, 2011) and it has lately been used with some consistency in the herpetocultural literature (Henkel 2009; Kaverkin 2009). Vences *et al.* (2001) found a small difference (4 bp) between Île des Pins and Grande Terre (Mt. Koghis) samples. We sampled specimens from three locations: Mt. Aoupinié in central New Caledonia, an apparently isolated population from sclerophyll forest at Presqu’île de Pindaï on the west coast, and Îlot Môrô, off the Île des Pins. Divergence between the two mainland populations was nearly as great as that between the most divergent populations of *R. auriculatus* but the divergence from these to the Îlot Môrô sample are twice as great. Although not included by us, Good *et al.* (1997) studied a specimen from Mt. Gouémba (= Wô Bwa Wîwâ) in the far southeast of the Grande Terre and found that it differed by one fixed allozyme difference from Mt. Aoupinié specimens.

De Vosjoli *et al.* (2003) had suggested that the mainland and southern insular populations were distinct species based on differences in size, morphology and behavior. As noted by Seipp and Henkel (2000, 2011) the population from the region of the Île des Pins, the type locality of *R. t. trachycephalus*, differs in a number of ways from typical *R. t. trachyrhynchus*, which are known from scattered localities across the Grande Terre (Fig. 6). These

include smaller size, a lower average number of scales in various counts, and a difference in the configuration of the head scalation. Myers and Pether (1998) suggested that Grande Terre animals were sometimes more yellowish than Île des Pins specimens, and differences in snout length have also been suggested (Henkel 1991, 1993 Myers & Pether 1998). Although the same arguments regarding the recency and transiency of gecko populations on the low-lying satellite islands around the Île des Pins applies to this form as to *R. l. henkeli*, the Île des Pins itself is a high island (maximum elevation 262 m) that would have remained above water since the Miocene and which would have been isolated from the Grande Terre sporadically since that time (Hope 1996). Issues of size aside, we believe that the deep genetic divergence and distinctive morphological features seen in the insular specimens are reflective of a meaningful evolutionary split and we recognize *R. trachycephalus* (Boulenger, 1878) (Figs. 7–8) as a valid species.



**FIGURE 6.** Distribution map of *Rhacodactylus trachyrhynchus* (green circles) and *R. trachycephalus* (red circle). The question mark on the Île des Pins represents numerous records of *R. trachycephalus*, including the types, that lack precise locality data. See Appendix for a list of localities mapped.

Boulenger's (1878) description is relatively detailed and is accompanied by a well-executed plate. His synonymization (1883) with *R. trachyrhynchus* is understandable given that the small number of individuals of both species then known did not allow a distinction between individual or population variation and specific differences. Boulenger's description was based on two specimens in the Institut Royal des Sciences Naturelles de Belgique in Brussels (Fig 7).

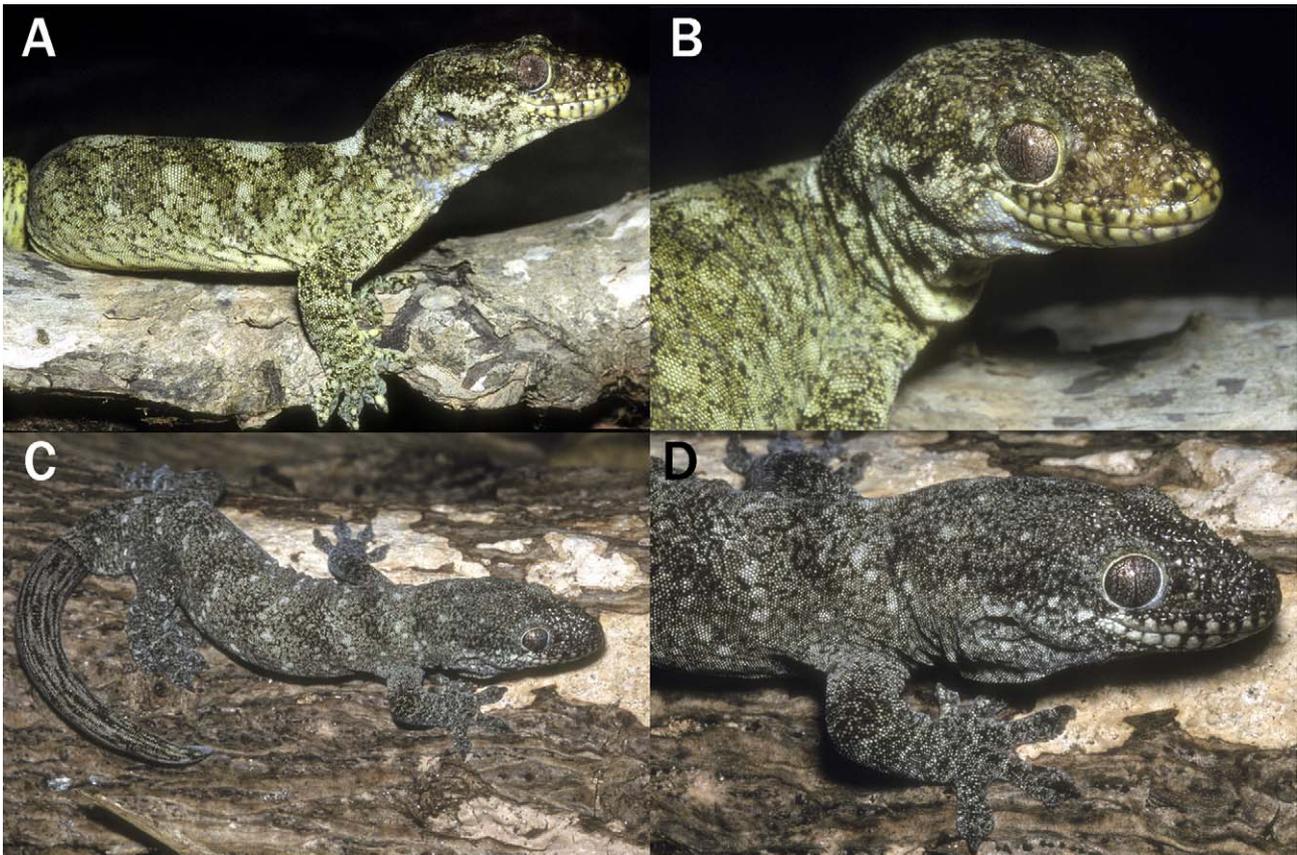
**Diagnosis.** *Rhacodactylus trachycephalus* may be distinguished from *R. trachyrhynchus*, the only other New Caledonian giant gecko with a rugose snout by its smaller size (maximum SVL 140 mm *versus* 190 mm), larger eye size relative to snout length and eye-ear distance, lower number of midbody scale rows (maximum 111 *versus* minimum 119) (*vide* Seipp & Henkel 2011), exclusion of the rostral from the nostril (*versus* rostral contacts the nostril or very narrowly excluded in *R. trachyrhynchus*), and smaller, less rugose scales in the loreal region (Fig. 8).

**Distribution.** Seipp and Henkel (2001, 2011) gave the distribution of this species as the Île des Pins and “Koutouma” [*sic*] (= Kûtomo), de Vosjoli (1997) reported it from “Island E,” and Vences *et al.* (2001) sequenced an individual supposedly from the Île des Pins. However, limited field investigations by Bauer and Sadlier (1994) and de Vosjoli (1995) could not verify its presence on the Île des Pins proper, although Bauer and Sadlier (1994) did identify appropriate habitat for the species on the island. We have encountered it only on Môrô, an island of ~0.1 km<sup>2</sup>, where its biology has been studied by Cunkelman (2005).



**FIGURE 7.** *Rhacodactylus trachycephalus* lectotype (IRSNB 2.532) and paralectotype (IRSNB 2.533) from Île des Pins (without precise locality). Photos courtesy of Georges Lenglet.

**Conservation.** de Vosjoli *et al.* (2003) highlighted *R. trachycephalus* as the only endangered *Rhacodactylus*. This species certainly has the most restricted range of any member of the genus. On Môrô they are especially vulnerable because of the easy access from the Île des Pins. *Rhacodactylus trachycephalus* is at very high risk due to potential demands from the pet trade. Most live-bearing *Rhacodactylus* offered for sale are members of this species (Kaverkin 2009). In comparison to most oviparous species, live-bearing *Rhacodactylus* have proven difficult to breed in captivity (Myers & Pether 1998) and they remain very expensive in the pet trade, with online prices of US\$3000 or more as of March 2012. This suggests there may remain a market for wild-caught individuals, a scenario which may no longer be true for some of the other giant geckos, which are now bred in great numbers in captivity and are available at relatively low prices. In addition to illegal collecting for the pet trade, this species is also likely to be highly vulnerable to introduced mammals, including rats and feral cats (Cunkelman 2005). Based on its extremely small area of occupancy and extent of occurrence as well as observed decline in habitat quality, as well as threats from introduced predators and the pet trade *R. trachycephalus* is assessed as Critically Endangered (B1b; B2b).

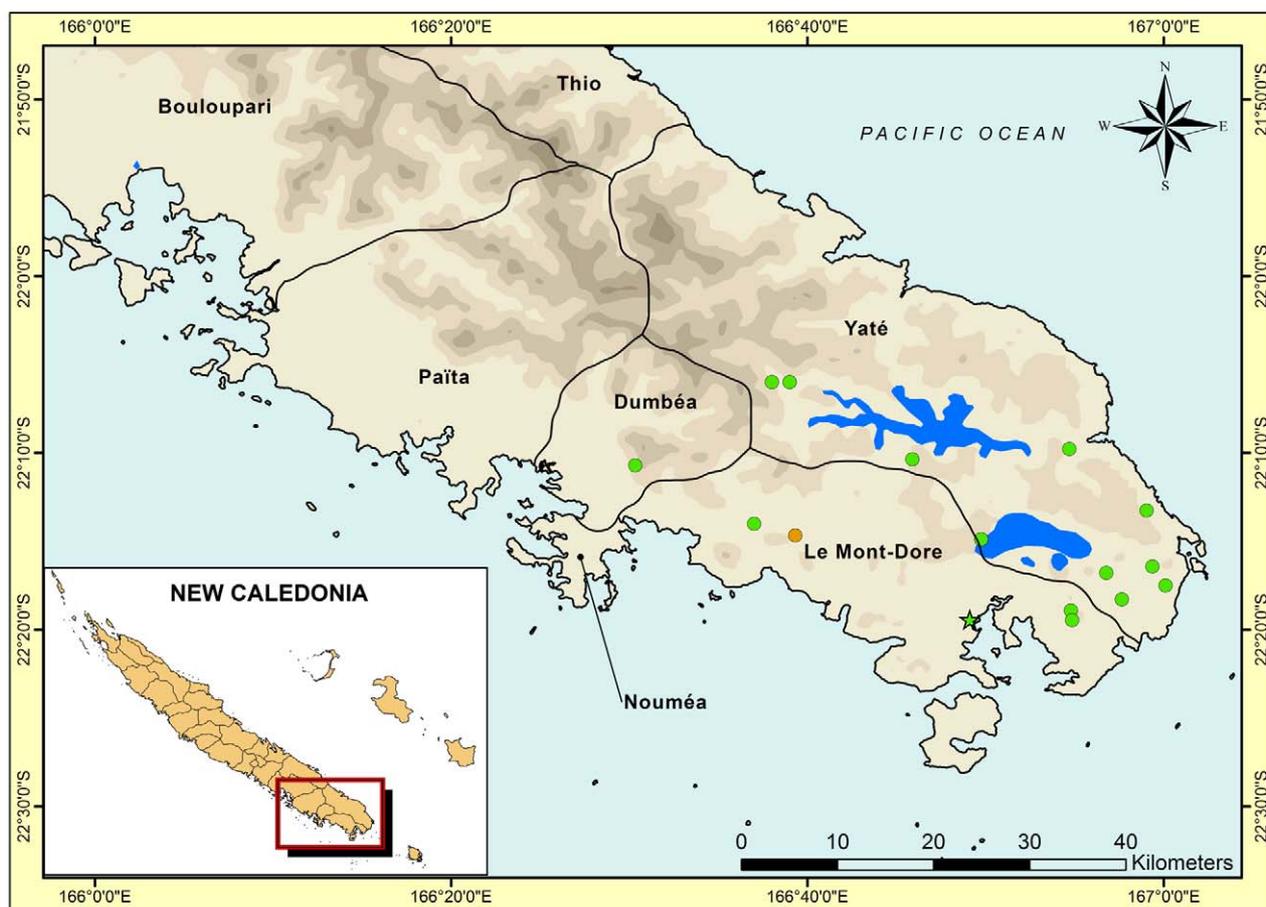


**FIGURE 8.** Living specimens of *Rhacodactylus trachyrhynchus* from Mt. Aoupinié, Province Nord, New Caledonia (A, B) and *R. trachycephalus* from Îlot Môrô, a small satellite island of the Île des Pins, Province Sud, New Caledonia (C, D). Photos courtesy of Mark O'Shea.

### Correlophus

*Correlophus sarasinorum* exhibits almost no intraspecific variation in the genetic markers we studied, even in the rapidly evolving mitochondrial genes (Figs. 1–2). This is perhaps not surprising given the very restricted distribution of this species, which is limited to the southern ultramafic block of the Grande Terre (Bauer 1990; Bauer & Henle 1994; Bauer & Sadlier 2000; Fig. 9). Within this limited variation specimens from Fôret Nord in the far south of the Plaine des Lacs differ only minimally from those further north at Mt. Koghis and Bois du Sud. Variation in color pattern has been previously mentioned (Böhme & Henkel 1985; Henkel 1987, 1988; Bauer 1990; Myers 1997) but this appears to have no obvious phylogenetic basis. Good *et al.* (1997) found four fixed allozyme

differences between single individuals of *C. sarasinorum* from Touaourou and Rivière Bleue, leading Bauer and Sadlier (2001) to hypothesize that two species might be represented. The information from the DNA sequence data presented here clearly contradicts this assumption and highlights the pitfalls of limited sampling. Several “morphs” are recognized by hobbyists (de Vosjoli *et al.* 2003), but these are also of no phylogenetic significance.



**FIGURE 9.** Distribution map of *Correlophus sarasinorum* in southern New Caledonia. Type locality indicated by a green star, other vouchers localities by green circles, orange circle indicates unvouchered record. See Appendix for a list of localities mapped. Named subdivisions are communes.

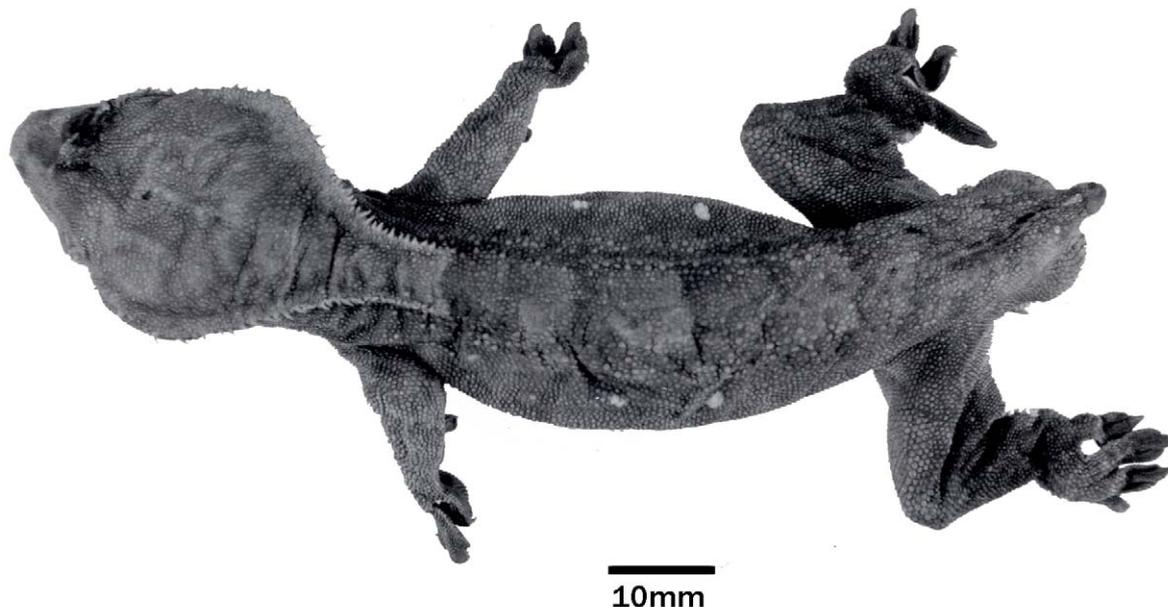
*Correlophus ciliatus*—The greatest intraspecific genetic divergence within any giant gecko was seen within *C. ciliatus* (Figs. 1–2). This species was described in 1866 (Fig. 10) and was apparently not uncommon in that era (Bavay 1869). It was then “lost” to science for over 100 years and considered likely to be extinct (Bauer & Sadlier 1993) until rediscovered on the Île des Pins in the 1990s (Storelli 1994; Seipp & Klemmer 1994; Kullmann 1995). It was subsequently found on several smaller satellite islands around Île des Pins (de Vosjoli 1995) and in the southern Grande Terre (Girard & Heuclin 1998; Bauer & Sadlier 2000, 2001; Fig. 11). Since then it has become one of the most popular of all lizard pets and is bred in at least the tens of thousands around the world (Baldwin & Repashy 1998; Both 1999; Bach 2006). All or most of these animals appear to originate from the Île des Pins, rather than Grande Terre. We found very little divergence between Île des Pins specimens and those from Rivière Bleue on the mainland, but quite deep divergences, comparable to the deepest within *R. auriculatus*, between these and a single specimen from Mt. Dzumac, only about 20 km distant from Rivière Bleue. However, specimens from the recently discovered population from the Îles Belep (Whitaker *et al.* 2004; Wirth & Peukert 2009) were as divergent as the most deeply-divergent splits between species in the *Bavayia sauvagii* clade.

Further, there are morphological differences between the southern and northern populations concordant with the genetic differences retrieved, lending further support to the recognition of the Belep Island populations as an independent evolutionary lineage, and on these criteria we here recognize this northern “*ciliatus*” as a new species:

***Correlophus belepensis* Bauer, Whitaker, Sadlier & Jackman sp. nov.**

(Figs. 12–15)

**Holotype.** MNHN 2011.1100 (formerly AMS 161281), adult male (Figs. 12–15). New Caledonia, Province Nord, Îles Belep, Île Art, 2 km E Waala, Wênè Cògat, 19°42'46.9" S, 163°39'37.7" E, 230 m. Collected 23 May 2002 by A.H. Whitaker and V.A. Whitaker.



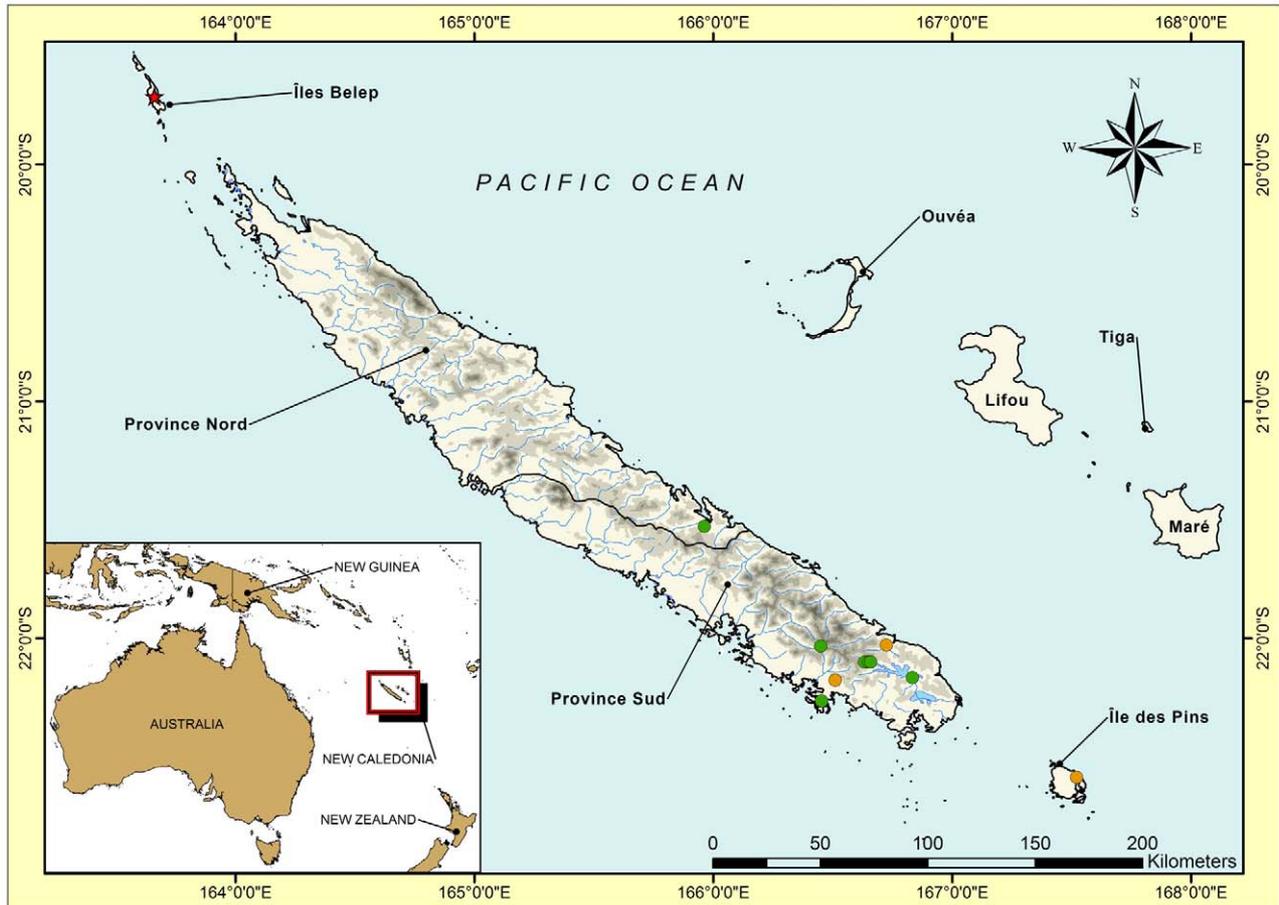
**FIGURE 10.** Lectotype of *Correlophus ciliatus* (MNHN 701A) showing the absence of lumbosacral tubercles and presence of heterogeneous dorsolateral scalation. Photo courtesy of Muséum National d'Histoire Naturelle, Paris.

**Paratypes.** AMS R161282–283, CAS 250865 (formerly AMS R161284) (Fig. 15). Data as for holotype.

**Diagnosis.** *Correlophus belepensis* sp. nov. is a large (to 100 mm SVL) diplodactylid. It differs from *C. sarasinorum* in possessing a prominent crest of spinose scales extending from behind the orbit to the shoulder region. It is most similar to its sister taxon *C. ciliatus*, but may be distinguished from it by its homogeneous dorsolateral trunk scalation (Figs. 12, 13A) (*versus* a raised and enlarged series of scales extending posteriorly from the end of the spinose crest, Fig. 10), and (in three of the four types) its possession of a series of small whitish tubercles on the lower back and/or tail base (Figs. 12, 13A, 14A, 15) (absent in *C. ciliatus*).

**Description.** (data from adult male holotype, MNHN 2011.1100). Specimen fixed with mouth open wide; abdominal incision for removal of liver sample for DNA. SVL 95.6 mm; TailL 11.6 (broken with minimal regeneration); TrunkL 39.4 mm; HeadL 27.4 mm; HeadW 21.6 mm; SnEye 11.2 mm; OrbD 7.1 mm; EyeEar 7.8 mm. Body moderately long (TrunkL = 41% SVL), slender, slightly depressed. Head triangular, large (HeadL = 29% SVL), very wide (HeadW = 79% HeadL), very well demarcated from neck (Fig. 12); nasofrontal region depressed, dorsal orbital rims raised; canthus distinct; snout relatively long (SnEye = 41% HeadL), much longer than eye diameter (OrbD = 64% SnEye). Scales on dorsum of snout approximately two to five times the diameter of those on occipital region, largest along canthus and immediately posterior to supranasals. Eye large (OrbD = 26% HeadL); pupil oval, margins faintly crenellated. Ear opening approximately two to three times longer than high, canted posterodorsally to anteroventrally at < 45° to the horizontal; eye to ear distance longer than diameter of eyes (EyeEar = 110% OrbD). Rostral rectangular, much broader (4.1 mm) than high (2.2 mm), without rostral crease, contacted posteriorly by three internasals — median smaller and pentagonal, lateral ones larger and hexagonal — and two large supranasals, each somewhat larger than the lateral internasals; contacted posteroventrally by first supralabial. Nostrils oval, laterally oriented, surrounded by eight circumnarial scales, including enlarged supranasal, and broadly contacted by first supralabial. Mental subtriangular, deeper (2.3 mm) than broad (1.7 mm). Two somewhat enlarged (6–8 times size of throat granules) postmental scales separate first infralabials from one another. Postmentals bordered posterolaterally and posteriorly by series of five smaller

(~50% size of postmentals) scales. Scales in two to five rows medial to infralabials somewhat enlarged and elongate. 13(left)–15(right) enlarged supralabial scales, posteriormost only about 3 times size of rictal scales, 10 (left) or 12 (right) supralabials to midpoint of orbit; 12 (left)–13 (right) enlarged infralabial scales (right infralabials 8–11 fragmented into two rows of scales); 38 scale rows between supraciliaries, 18 scale rows across frontal bones at midpoint of orbit. Supraciliary scales forming 17 (L) and 18 (R) large pointed spines, smaller anteriorly, largest posterodorsally and posteriorly.



**FIGURE 11.** Distribution map of *Correlophus ciliatus* (circles) and *C. belepensis* **sp. nov.** (red star). For *C. ciliatus* green circles symbols represent vouchered records, orange circles represent unvouchered sight or literature records. Vouchered records from the Île des Pins lack precise localities. See Appendix for a list of localities mapped.

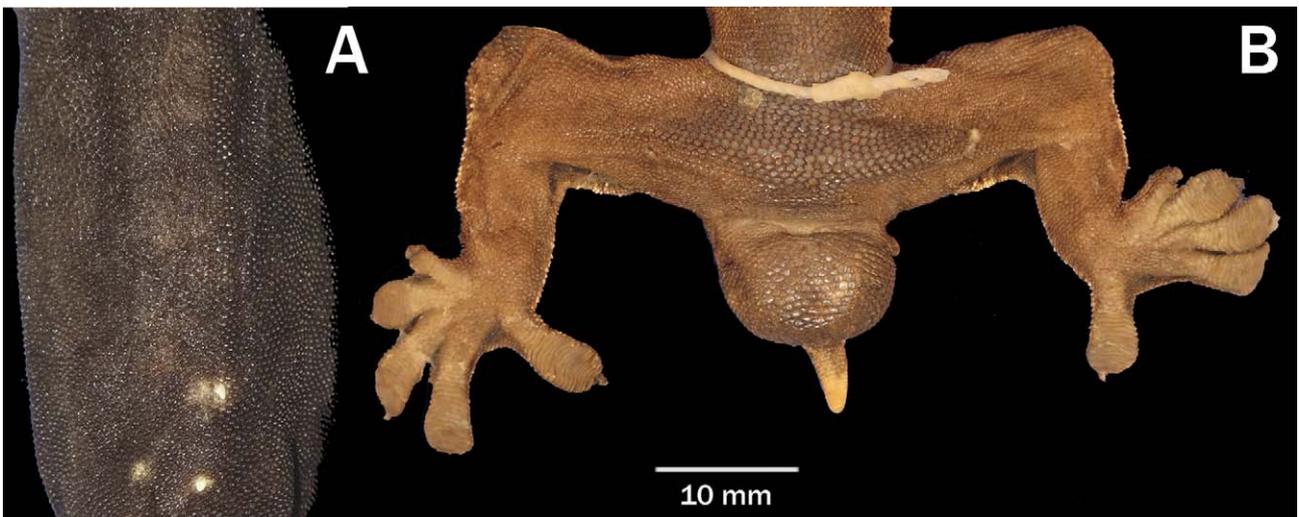
Dorsal scales small, mostly homogeneous (Figs. 12, 13A), conical; ventral scales 1.3–2 times size of dorsals, smooth, flattened, oval, juxtaposed to subimbricate, enlarged under sternum, midventrally on posterior abdomen, and in precloacal region. Sternal and posterior abdominal scales rounded. Approximately 154 scale rows around mid-body. A dorsolateral fold of skin from anterior to ear to approximately level of adpressed elbow, strongly projecting above ear and on neck, continuing posteriorly as a slightly raised crest. Entire fold/crest bearing elongate spinose scales, becoming smaller above shoulder; a few small, scattered spinose scales between anterior margin of fold and posteriormost spinose supraciliaries. Lumbosacral region with six scattered, enlarged, semi-erect conical white tubercles, with their apices directed posteriorly or posterolaterally. Another two such tubercles at tail base, followed posteriorly by several slightly enlarged and irregularly-shaped non-tuberculate scales.

Skin folds small but distinct on ventrolateral trunk between limb insertions, on ventrolateral border of neck, and on posterior margins of forelimbs. Well developed folds along postaxial border of hindlimbs, forming deep popliteal pockets behind the knees (Fig. 13B). Scales on postaxial hindlimb fold as far as base of digit V of pes with scattered, white, conical to weakly spinose tubercles. Scales on limbs granular to low and conical, subimbricate to juxtaposed. Scales on palms and soles smooth, flattened. Fore- and hindlimbs, exclusive of skin folds, moderately long and slender (ForeaL = 14% SVL; CrusL = 18% SVL), axillary pocket weakly developed.

Digits moderately long, all bearing claws, those on digit I of both manus and pes reduced and partially sheathed, remaining claws long and strongly recurved; relative length of digits of manus: IV>III>II>V>I, and of pes: IV>III>V>II>I; digits well webbed; digits III and IV of pes tightly bound along length of elongate metatarsals. Subdigital lamellae all unpaired, somewhat bowed, with lateral margins gently angled distally (except for proximalmost lamellae, which are straight). Claw of digit I of manus and pes, lies between a smaller lateral and a larger (twice size of lateral) medial apical scansor. Lamellar counts from right (and left) sides 10-13-17-18-15 (10-15-18-17-15) manus and 12-15-17-20-18 (12-14-18-19-17) pes (excludes apical scansors of digit I).



**FIGURE 12.** Preserved holotype (MNHN 2011.1100) of *Correlophus belepensis* **sp. nov.** from Île Art, Îles Belep. Photo by A.M. Bauer.



**FIGURE 13.** Holotype (MNHN 2011.1100) of *Correlophus belepensis* **sp. nov.** showing (A) homogeneous dorsal sculation and (B) rudimentary regenerated tail, skin folds on posterior margin of thighs, and preloacal pores extending onto thighs (the three pore-bearing rows of scales are near the posterior margin of the grayish patch of scales anterior to the vent). Photos by A.M. Bauer.

Small preloacal pores in a patch of somewhat enlarged scales, arranged in three rows (anterior to posterior), each divided by two small poreless scales medially, of 15(L) + 15(R), 12(L) + 10(R), and 3 (L) + 4(R). Pores

restricted to proximal 40% of thighs (Fig. 13B). Hemipenial bulge large; a single large, smooth, flattened, conical cloacal spur comprising a much larger dorsal scale and a small posterolateral scale subtending it on each side of tail base. Tail broken at base and supporting a rudimentary regenerate of narrow diameter (see Discussion).

Color in preservative (based on holotype): Dorsum, lateral surfaces of trunk, side of neck and head posterior to orbit, and limbs more-or-less a uniform dark chocolate brown. Snout, dorsum of head and middorsal region between dorsolateral spinose crests a lighter brown with a tinge of brick red (Fig. 12). Posterior infralabial scales with whitish ventral borders. Midvertebral region between end of spinose crests and white tubercles of lumbar region mottled with some hint of alternating lighter and darker brown bands. Venter light brown with darker mottling, especially on anterior chest, mid- to posterior abdomen, in precloacal region, and under hemipenial bulge. Soles and palms pale grayish brown. A white line along the postaxial margin of the hindlimb. Tail base bearing a cream “Y”-shaped marking dorsally; vestigial regenerated tail beige with dark pigment around its base.

In life the dorsal coloration of the types was an orangey-brown with a slightly greenish suffusion, with darker diffuse irregular reticulations on the flanks. Crown of the head, area between denticulate crests, and anterior mid-dorsal region more distinctly orangey to russet than adjacent flanks, fading either abruptly or gradually posterior to the shoulders. Anterior of head with yellowish highlights; orbital rim and ventrolateral surfaces of supraciliary scales yellow. Iris silvery to whitish (Fig. 14). Venter reddish-brown, with diffuse, darker gray-brown irregular markings, particularly along the ventrolateral margins and with scattered isolated greenish-yellow scales. Tongue and interior of mouth unpigmented.



**FIGURE 14.** Life photographs of *Correlophus belepensis* sp. nov. (A) Male holotype (MNHN 2011.1100) and (B) smaller female paratype (CAS 250865). Photos by A.H. Whitaker.

**Osteology.** Vertebral counts are typical for diplodactylid geckos, with 26 presacral and 2 sacral vertebrae. The first three cervical vertebrae are without ribs, as is the last presacral (lumbar) vertebra. Also typical for the family, the caudal skeleton includes 5 pygal vertebrae. The holotype and all paratypes have the tail broken within the first postpygal vertebra. The phalangeal formulae of the manus and pes are unreduced, 2-3-4-5-3 and 2-3-4-5-4, respectively. Total tooth loci in upper jaw of holotype 85, of which 9 in premaxilla; total mandibular tooth loci 78. A single pair of crescentic cloacal bones is present in the holotype and in the male paratype AMS R161282. In both female paratypes the endolymphatic system is visible in x-rays by its radio-opaque calcium content and can be seen to be entirely intracranial.

**Variation.** Comparative mensural and meristic data for the holotype and paratypes are given in Table 2. Meristic characters of paratypes are mostly similar to those of the holotype, and are mentioned hereafter if only they differ. All paratypes had only a single postmental scale. AMS R161283 had seven circumnarial scales and CAS 250865 had seven around the left naris and eight around the right. Precloacal pores are arranged in rows of 18(L) + 15(R), 10(L) + 10(R), and 3(L) + 2(R) in the male paratype (AMS R161282) and are absent in the female paratypes. In the male paratype the posterolateral scale of the cloacal spur is separate from the larger scale, resulting in two discrete cloacal spurs on each side of the tail base. In the females the cloacal spurs are represented by one to three slightly enlarged smooth conical scales.

**TABLE 2.** Mensural data for the types of *Correlophus belepensis* **sp. nov.** Abbreviations as in Materials and methods. All measurements in mm. \* All tails broken with rudimentary regenerated tips.

	MNHN 2011.1100	AMS R161282	AMS R161283	CAS 250865
	holotype	paratype	paratype	paratype
Sex	male	male	female	female
SVL	95.6	88.6	99.7	99.4
ForeaL	13.4	12.1	13.0	12.3
CrusL	17.2	15.3	16.7	16.4
TailL*	11.6	12.9	15.0	16.4
TrunkL	39.4	34.5	40.6	41.0
HeadL	27.4	25.4	29.6	27.8
HeadW	21.6	19.8	22.4	22.0
OrbD	7.1	6.8	7.6	7.0
EyeEar	7.8	7.5	8.8	8.0
SnEye	11.2	11.1	11.8	11.7
NarEye	8.0	8.2	8.5	8.5
Interorb	11.3	10.3	13.2	13.9
EarL	2.2	1.3	1.9	occluded
Internar	3.3	3.2	3.4	3.7
SupraL L/R	13(10)/15(12)	15(12)/ 16(13)	14(11)/ 14(11)	15(12)/ 14(11)
InfraL L/R	12/13	13/13	13/14	13/13
LamManus L/R	10-15-18-17-15/10- 13-17-18-15	14-15-16-19-15/ 13-14- 16-19-15	11-14-17-19-15/ 10- 14-18-18-15	9-13-17-20-14/ 11- 13-16-17-15
LamPes L/R	12-14-18-19-17/12- 15-17-20-18	13-16-18-19-18/ 13-15- 17-21-17	10-13-16-19-17/ 10- 15-19-21-17	8-14-19-19-17/ 10- 15-18-21-17

Color pattern is generally similar among all specimens examined, although in AMS R161282 and CAS 250865 the dark chocolate dorsal and lateral coloration is more mottled and less uniform than in the holotype. The number of white tubercles on the dorsum is also variable (Fig. 15). AMS R161283 has three tubercles on the lumbosacral region, two to the left of the midline and one to the right. In AMS R161282 there is a single such scale anterior to the hindlimb insertion and left of the dorsal midline and several irregular scales, including one small white tubercle at the tail base, but neither tubercle is conical as in the holotype. In CAS 250865 there are no lumbosacral tubercles. Venter in life yellowish (CAS 250865) to reddish-brown; females lacking the scattered greenish-yellow ventral scales of males.

**Etymology.** The specific epithet refers to the Îles Belep, to which this species is apparently restricted.

**Distribution.** *Correlophus belepensis* has been recorded only from Île Art, in the Îles Belep group more than 40 km north-west of Grande Terre (Whitaker *et al* 2004; Fig. 11)). Two discrete sub-populations occur on Île Art, 4.5 km apart, one on the Tolé Munu plateau (c.700 ha) and the other on the Kalidan plateau (c. 220 ha). The type series was collected on the former; specimens were observed, but not collected, at Puröbi (19°45'06.1"S, 163°40'29.0"E, 230 m) on the latter. These plateaux comprise an undulating ultramafic substrate between 220–250 m in elevation that is capped by a rocky cuirasse surface covered with closed forest or paraforestier. They are separated by a wide, low saddle (<90 m) with sparse fire-induced savannah woodland and grassland. A small area (c.90 ha) of similar habitat to that on the Tolé Munu and Kalidan plateaux occurs at lower elevation (140–150 m) on Île Pott, the only other large island in the Belep group, but it has not been surveyed.

**Natural History.** *Correlophus belepensis* has only been found in old-growth, low-stature (<10m) closed humidforest and paraforestier habitat (<8 m) on bouldery cuirasse surfaces (Fig. 16). The Tolé Munu plateau has a

diverse flora (>170 species) including several rare and threatened taxa, several of which are endemic to that site (Munzinger *et al.* 2009). Dominant canopy trees in this forest, with large trunks with holes and crevices as retreat sites for geckos, are *Ficus prolixa* G. Forst. (Fam. Moraceae), *Alphandia resinosa* Baill. (Fam. Euphorbiaceae), *Iteiluma* sp. (Fam. Sapotaceae), *Planchonella wakere* (Pancher & Sebert) Pierre (Fam. Sapotaceae), *Mimusops elengi* L. (Fam. Sapotaceae), and *Piliocalyx laurifolius* Brongn. & Gris and *Piliocalyx* sp. (Fam. Myrtaceae). Fortuitously, browsing ungulates and pigs are absent from the Belep Islands so this forest is in reasonably good condition with thick undergrowth. All observations of *C. belepensis* have been at night while they are active and it appears to be an exclusively arboreal species. Unlike *Mniarogekko jalu* n. sp., with which it is syntopic, *C. belepensis* was found at all levels within the forest from the upper surface of the canopy to low in sub-canopy and forest margin shrubs. Perches used were similarly varied and included foliage, twigs, branches and trunks. The new species is particularly agile when moving through the vegetation and frequently leaps between branches, as much as 30 cm vertically upwards and >40 cm horizontally. When threatened they jump from the canopy or other vegetation and fall, spread-eagled and horizontal, to lower plants or the forest floor. If pursued on the ground they move in a series of frog-like leaps, up to 12 cm high and covering 30–40 cm in each bound. A similar tendency to jump has been documented in its sister species *C. ciliatus* (Vosjoli *et al.* 2003).



**FIGURE 15.** Type series of *Correlophus belepensis* sp. nov. showing variation in color and in lumbar and sacral tubercles. Left to right: holotype (MNHN 2011.1100), paratypes (AMS R161282, AMS R161283, CAS 250865). Photo by A.H. Whitaker.

On Île Art *C. belepensis* is syntopic with *Mniarogekko jalu* n. sp., *Eurydactylodes agricolae* and *Dierogekko insularis*. Species sympatric within its habitat include *Kanakysaurus viviparus* Sadlier, Smith, Bauer & Whitaker, 2004, *Lioscincus nigrofasciolatus* (Peters, 1869), *Caledoniscincus atropunctatus* (Roux, 1913), *C. austrocaledonicus* (Bavay, 1869), and *C. haplorhinus* (Günther, 1872), and *Bavayia* aff. *cyclura*, *Hemidactylus frenatus* Schlegel in Duméril & Bibron, 1836, *Lepidodactylus lugubris* (Duméril & Bibron, 1836), and *Phoboscincus garnieri* (Bavay, 1869) were recorded in adjacent savannah and secondary shrubland.

Trombiculid mites are present between the subdigital lamellae and in one or both popliteal pockets in all of the specimens examined.

**Conservation status.** *Correlophus belepensis* has been recorded only on Île Art, in the Belep archipelago, where it occurs as two sub-populations within a single locality. It is expected that the species may also occur in similar habitat on nearby Île Pott. Whether its entire distribution is confined to the Belep archipelago is unclear but at present there is no evidence of populations on the mainland.



**FIGURE 16.** Habitat of *Correlophus belepensis* **sp. nov.** and *Mniarogekko jalu* **sp. nov.** on the Tolé Munu plateau, Île Art, Îles Belep, Province Nord, New Caledonia. Photo by A.H. Whitaker.

Within the known extent of occurrence for *C. belepensis*, the closed forest and paraforestier formations on cuirasse surfaces are surprisingly intact given the high level of habitat modification that has occurred elsewhere on Île Art. Both plateaux are still largely covered by forest, but as a result of repeated burning and clearance for subsistence gardening since colonization by Melanesians, the surrounding slopes and remainder of the island have been modified and are characterized by depleted niaouli (*Melaleuca quinquenervia* (Cav.) Blake, Fam. Myrtaceae) savannah, secondary shrublands and grassland. This is assumed to have resulted in a contraction of the area of occupation for this species.

The sub-populations of *C. belepensis* on Île Art are at risk to several direct and indirect threats. Wildfires regularly affect large areas of the grassland, savannah and shrubland, and these inevitably encroach on the remaining forest, reducing it in extent. There is also sporadic timber cutting for local use but to date this has had only a very localized impact. Introduced rats (*Rattus* spp.) and feral cats are present throughout the habitat. Both are known to be predators of lizards but no direct evidence of predation on *C. belepensis* was obtained. Little red fire ants, *Wasmannia auropunctata* (Roger, 1863) are also present in the forest on the plateaux. These highly-invasive ants are known to have a severe detrimental impact on lizard populations (Jourdan *et al.* 2000, 2001). *Hemidactylus frenatus* has colonized the Îles Belep relatively recently and was detected in the township of Waala, as well as in littoral vegetation, garden sites and savannah woodlands. If it spreads into forest habitat, as is expected, it is unclear what impact this invasive gecko would have on giant gecko species but elsewhere it is known to result in competitive exclusion and local extirpation of smaller indigenous geckos (e.g., Case *et al.* 1994; Petren *et al.* 1993; Petren & Case 1996; Cole *et al.* 2005; Rivas *et al.* 2005).

The ultramafic plateaux on both Île Art and Île Pott have been subjected to extensive prospecting in the past and are criss-crossed by old access tracks and drill sites. Although these areas are held under current mining licenses there appear to be no immediate plans to exploit the areas. However, should it occur, mining would almost certainly remove a significant proportion—if not all—of the available habitat for this species.

No quantitative data on population size and trends are available for *C. belepensis*. In 2001 it was relatively abundant in the forest on the Tolé Munu plateau, with encounter rates of 0.57–0.83/person hour, implying a population density approximately half that of the syntopic *Mniarogekko jalu* **n. sp.** (Whitaker *et al.* 2004).

Because of its extremely limited extent of occurrence (<25 km<sup>2</sup>) and area of occupation (<10 km<sup>2</sup>), presence at a single locality, the threats to its habitat (wildfires, and perhaps mining), the presence of mammalian predators (rats, cats) and the impacts of fire ants, *Correlophus belepensis* is assessed as Critically Endangered (B1a, b[i–iii, v]; B2a, b[i–iii, v]) (IUCN 2001).

**Remarks.** *Correlophus ciliatus* occurs in southern Grande Terre and on the Île des Pins, with a northern known limit of range around 300 km south-east of the Îles Belep (Bauer & Sadlier 2000; Fig. 11). The presence of these two taxa at either end of Grande Terre suggests the occurrence of *C. belepensis* is relictual and that it is not a primary endemic in the Belep group, but extensive fieldwork in the northern Grande Terre has not revealed any *Correlophus*.

Although the diagnostic heterogeneous paravertebral trunk scalation of *C. ciliatus* is not illustrated in the type illustration of that species (Guichenot 1866), it is clearly visible in the lectotype specimens (Fig 10) and in published photos of the species (e.g., Seipp & Klemmer 1994; Gerard 1999; Seipp & Henkel 2001, 2011; Bauer & Sadlier 2000; de Vosjoli *et al.* 2003; Bach 2006; Henkel & Schmidt 2007; Hamper 2003; Wirth & Peukert 2009; Sommer 2009).

### ***Mniarogekko* gen. nov.**

*Mniarogekko chahoua* — No subspecies have been described and no synonyms exist for *Mniarogekko chahoua*, nor have previous authors discussed intraspecific variation in the context of possible taxonomic significance. However, our results reveal relatively large intraspecific divergence within this taxon (Figs. 1–2). Seipp and Henkel (2000) first noted that *M. chahoua* occurred in far northern New Caledonia, northeast of Koumac, and speculated that the species might be distributed island-wide. Specimens from this same population, at Rivière Néhoué, were reported on extensively by Langner (2009). *Mniarogekko chahoua* specimens from recently discovered northern populations on Île Art in the Belep group and at Vallée Poupoule, Dôme de Tiébaghi, and Rivière Néhoué in the far northwest of the Grande Terre (Whitaker *et al.* 2004; Bauer *et al.* 2006b) are morphologically similar to one another but 7.8% divergent with respect to more southern Grande Terre specimens from Sarraméa and the Vallée d’Amoa. Specimens from these latter two localities are likewise highly genetically divergent from one another, but existing sample sizes are small and morphological differences between them have not yet been identified. All northern samples come from ultramafic areas, whereas those from the east-central and more southern Grande Terre populations are from low elevation (vallicole) habitats on non-ultramafic substrates (Fig. 17). Bauer (1985) reviewed *M. chahoua*, then known from very few specimens, and designated a specimen from the Vallée d’Amoa as the neotype (many captive *M. chahoua* supposedly derive from Île des Pins stock and these are stated by herpetoculturalists to differ from Grande Terre *M. chahoua*; however, we have not encountered *Mniarogekko* on the Île des Pins and have not examined museum specimens from this locality, therefore, we are unable to evaluate their taxonomic status). We believe that genetic and morphological differences warrant the description of a second *chahoua*-like species to accommodate the northern populations sampled here. This is described below:

### ***Mniarogekko jalu* Bauer, Whitaker, Sadlier & Jackman sp. nov.**

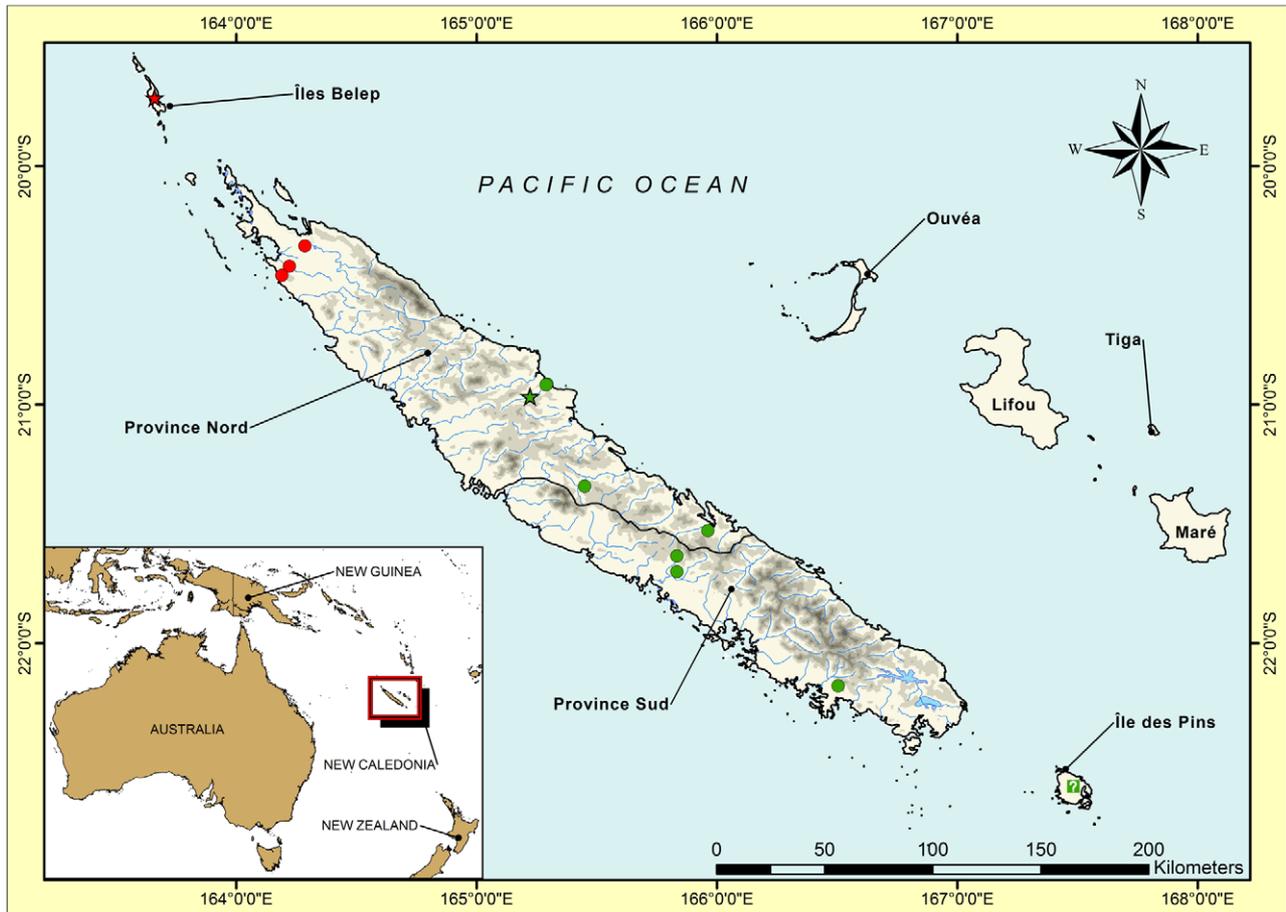
(Figs. 18–21)

**Holotype.** MNHN 2012.0211 (formerly AMS R161289), adult male (Fig. 18). New Caledonia, Province Nord, Îles Belep, Île Art, 2 km E Waala, Wênè Cogat, 19°42'46.9" S, 163°39'37.7" E, 230 m. Collected 28 May 2002 by A.H. Whitaker and V.A. Whitaker.

**Paratypes.** AMS 161285, subadult female, same data as holotype; AMS R161286, adult male, R161287–288, adult females, data as for holotype, but collected 23 May 2002; AMS R161224, adult male, New Caledonia, Province Nord, 24 km N Koumac, Forêt d’Ougne, Vallée Poupoule, 20°20'04.0"S, 164°17'07.1"E, 5 m, collected 15 October 2001 by A.H. Whitaker and V.A. Whitaker; AMS R161237–38, adult males, New Caledonia, Province Nord, 11 km NW Koumac, Dôme de Tiébaghi, 20°27'27.9"S 164°11' 22.8"E, 360 m, collected 17 October 2001 by A.H. Whitaker and V.A. Whitaker; CAS 250858–59, adult females, New Caledonia, Province Nord, 15 km N Koumac, Rivière Néhoué, 20°25'09.7"S, 164°13'16.3"E, 8 m, collected 22 January 2003 by A.M. Bauer, R.A. Sadlier, T.R. Jackman, G. Watkins-Colwell, and S.A. Smith.

**Diagnosis.** *Mniarogekko jalu* n. sp. is a large (to 140 mm SVL) diplodactylid. It may be distinguished from its sister taxon *M. chahoua* by its much lower number of precloacal pores in males (< 95 [range 54–91] versus ~120)

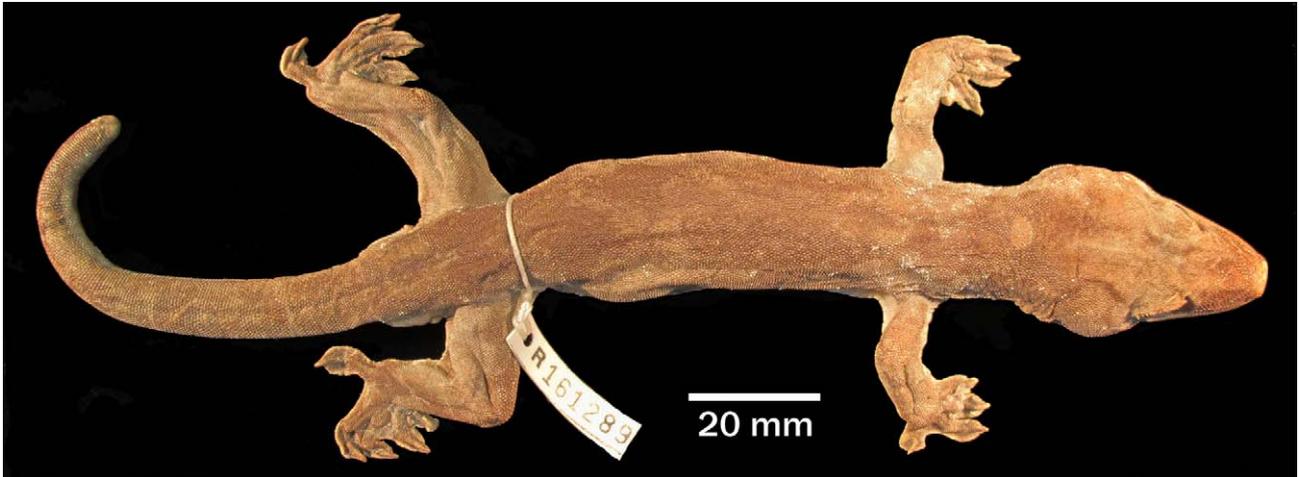
typically arranged in three (Fig. 19), rather than four rows. Color comparisons between the two species of *Mniarogekko* are difficult to make. There are relatively few wild caught *M. chahoua* in museum collections and captive animals have been bred for particular color patterns (de Vosjoli *et al.* 2003) so ‘wild type’ coloration, which is itself already quite variable (Bauer 1985; Seipp & Henkel 2000, 2011; Stark 2006; Langner 2009), is difficult to characterize. Ventral body coloration in the new species seems to be uniformly a pale yellowish green (Figs. 19–20), whereas *M. chahoua* is often white or cream, with a greenish tinge localized to some parts of the venter.



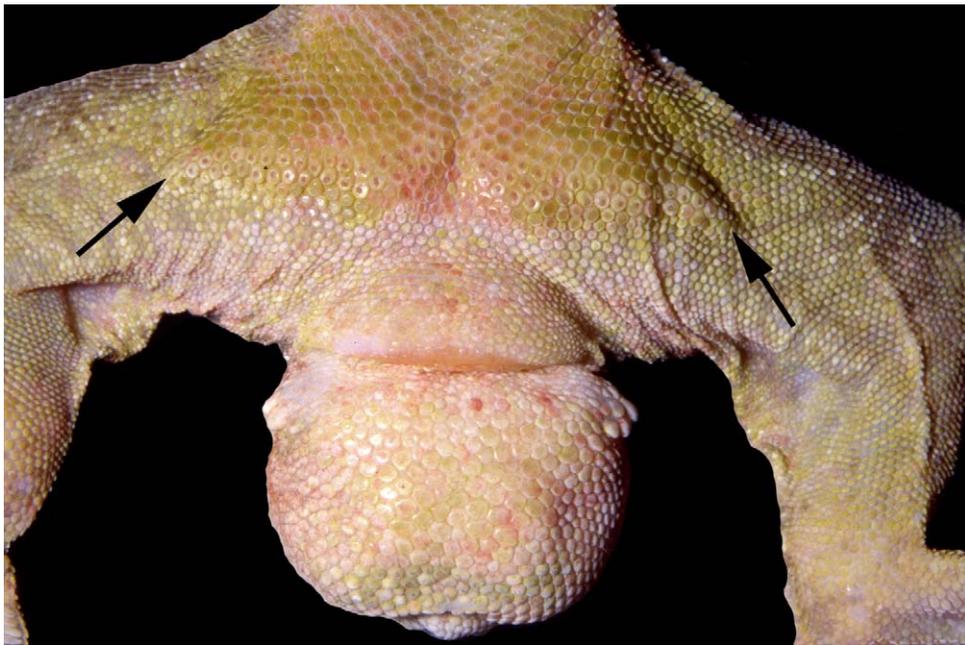
**FIGURE 17.** Distribution map of *Mniarogekko chahoua* (green symbols) and *M. jalu* **sp. nov.** (red symbols). Type localities are marked by stars. The question mark on the Île des Pins represents numerous literature records for *M. chahoua* that lack precise locality data. See Appendix for a list of localities mapped.

**Description.** (data from adult male holotype, MNHN 2012.0211). Specimen fixed with mouth open wide; abdominal incision for removal of liver sample for DNA. SVL 123.3 mm; TailL 76.2 mm (of which 19.0 mm are regenerated); TrunkL 51.9 mm; HeadL 32.4 mm; HeadW 22.8 mm; SnEye 12.6 mm; OrbD 7.0 mm; EyeEar 10.6 mm. Body moderately long (TrunkL = 42% SVL), robust, slightly depressed. Head oblong, large (HeadL = 26% SVL), wide (HeadW = 70% HeadL), well demarcated from neck (Fig. 18); nasofrontal region somewhat depressed; canthus prominent; snout relatively long (SnEye = 39% HeadL), much longer than eye diameter (OrbD = 56% SnEye). Scales on dorsum of snout approximately two times the diameter of those on occipital region. Eye relatively small (OrbD = 22% HeadL); pupil oval, margins crenellated. Ear opening approximately two times longer than high, canted posterodorsally to anteroventrally at  $< 30^\circ$  to the horizontal; eye to ear distance much longer than diameter of eyes (EyeEar = 150% OrbD). Rostral rectangular, more than twice as broad (5.3 mm) as high (2.3 mm), a very short rostral crease dorsally, contacted posteriorly by three small pentagonal internasals and two large supranasals, each approximately three times the size of larger (lateral) internasals; contacted posteroventrally by first supralabial. Nostrils oval to round, laterally oriented, surrounded by rostral, five (left) to seven (right) circumnarial scales, including enlarged supranasal, and narrowly contacted by first supralabial. Mental triangular, as deep as broad (3.2 mm). First infralabials somewhat elongate, narrowly separated from one

another posterior to the mental by a small, irregular postmental scale. Scales in four to five rows posterior to anterior infralabials and three to five rows medial to posterior infralabials slightly enlarged and elongate (3–5 times size of throat granules. 12(right)–14(left) enlarged supralabial scales, posteriormost only about 3 times size of rictal scales, 10 supralabials to midpoint of orbit; 12 (right)–13 (left) enlarged infralabial scales; 44 scale rows between supraciliaries, 21 scale rows across frontal bones at midpoint of orbit. Supraciliary scales forming a denticulated row, posterior two thirds of scales distinctly spiny.



**FIGURE 18.** Preserved holotype (MNHN 2012.0211) of *Mniarogekko jalu* **sp. nov.** from Île Art, Îles Belep. Photo by A.M. Bauer.



**FIGURE 19.** Ventral view of cloacal region of freshly euthanized male paratype (AMS R161224) of *Mniarogekko jalu* **sp. nov.** from Forêt d'Ougne, Vallée Poupoule, Province Nord, New Caledonia showing the extent of the rows of precloacal pore-bearing scales (arrows) and the greenish tinge of the venter. Photo by A.H. Whitaker.

Dorsal scales small, weakly heterogeneous, domed to weakly conical, oval to rounded, highest point slightly posterior of center, each separated from one another by a rosette of six surrounding triangular scales; ventral scales ~1.5 times diameter of dorsals, smooth, flattened, subimbricate, enlarged in precloacal region. Posterior abdominal scales rounded, mid-abdominal scales slightly elongate. Approximately 189 scale rows around mid-body. Well-defined non-denticulate ventrolateral skin folds from just anterior to angle of jaw to anterior thigh. Distinct folds on anterior and posterior margins of forelimb almost to base of palm; postaxial margin of hindlimb with fold from base of thigh to ankle. Scales of fore limbs not differing from dorsals, although slightly subimbricate near limb

insertion; scales of hind limbs subimbricate near limb insertion, distally, near ankle, granular and in regular rows, without rosettes of triangular interscales. Scales on palms and soles smooth, flattened. Fore- and hindlimbs short and thick (ForeaL/SVL ratio 0.12; CrusL/SVL ratio 0.15), axillary pocket well developed. Digits short, all bearing claws, those on digit I of both manus and pes reduced and partially sheathed, remaining claws long and strongly recurved; relative length of digits of manus: IV>III>V>II>I, and of pes: IV~V~III>II>I; digits moderately webbed; digits III and IV of pes tightly bound along length of elongate metatarsals. Subdigital lamellae all unpaired, somewhat bowed, with lateral margins gently angled distally (except for proximalmost ones which are straight, particularly in digit I). Claw of digit I, manus and pes, lies between a smaller lateral and a larger (twice size of lateral in manual digit, four times larger in pedal) medial apical scissor. Lamellar counts from right (and left) sides 13-16-19-21-14 (12-18-20-19-17) manus and 12-18-16-18-15 (13-16-19-19-15) pes (excludes apical scissors of digit I).

Large precloacal pores in a patch of somewhat enlarged scales, arranged in two rows (anterior to posterior) of 21 (L) + 20 (R), and 17 (L) + 18 (R), with left and right sides separated by a single poreless scale. Posterior row fragmented with some poreless scales separating pored scales on each side of ventral midline. Pores extend only on to very base of thighs. Hemipenial bulge large; cloacal spurs on raised base just posterior to hindlimb insertion, with a single very large, flattened, conical, posterodorsolaterally-directed scale subtended by a series of two (right) or 3 (left) smaller scales of similar form. Tail (approximately 25% regenerated in holotype) 62% of snout-vent length, thick, roughly round in cross-section, with a distinct longitudinal dorsal crease. Caudal scales small, flat, juxtaposed (proximally) to weakly subimbricate (distally), squarish to rectangular with rounded free margins, arranged in regular rows. Surface of tail weakly segmented, caudal scale rows forming whorls, each whorl 8 dorsal scale rows and 6 ventral scale rows long; ventral caudals 1.5–4.0 times larger than dorsals, midventral caudal scales not enlarged. Midventral scales of pygal region smaller than those of post-pygal region. Rows of scales on regenerated portion of tail not arranged in segments, with some irregular scales.

Color in preservative (based on holotype): Dorsum a mottled mid-brown with slightly lighter irregular transverse markings over shoulder and posterior abdomen (Fig. 18). A dark triangle over occiput and nape, with its apex directed posteriorly. Irregular darker brown patches over lumbar region and posterior sacrum. A small, oval reddish-brown spot on nape just left of center. Scattered white scales forming isolated patches of speckling from the posterior border of the orbit, above and below the ear, along neck and on to shoulder, where they are dense enough to form a broken shoulder patch. Additional scattered white scales forming scattered clusters along the trunk, mostly on flanks, across sacrum, and on pygal portion of tail.

Muzzle and occiput darker brown; crown grayish brown, similar to lighter transverse markings on trunk. A pale, diffuse, whitish line extending from posteriormost corner of orbit towards ear. Labial scales beige with slightly darker margins. Limbs similar to dorsum, with irregular, alternating lighter grayish and darker grayish-brown markings; a narrow band of white scales at junction between each set of alternating markings on forelimbs. Palms and soles grayish-cream. Tail roughly same color as dorsum, with mottling of brown and grayish-brown and several thin grayish-white bands.

Venter cream with incomplete, diffuse, pale brown transverse chevrons that are continuous laterally with markings on ventrolateral folds, forming a barred pattern along the fold between the limb insertions. Tail venter pale brown with some narrow pale bands. See Variation for a discussion of coloration in life.

**Osteology.** Vertebral counts are typical for diplodactylid geckos, with 26 presacral and 2 sacral vertebrae. The first three cervical vertebrae are without ribs, as is the last presacral (lumbar) vertebra. The caudal skeleton typically includes 5 pygal vertebrae, although only 4 are present in CAS 250859. Paratypes CAS 250858–59, AMS R 161237–38, 161224, 161286, and 161288 have the tail autotomized in the first post-pygal vertebra. In AMS R161287 the tail is autotomized in the second post-pygal vertebra. MNHN 2012.0211, the holotype, has a nearly complete tail, whereas AMS R 161285 has a complete tail with 27 post-pygal vertebrae. The holotype and all paratypes have the tail broken within the first postpygal vertebra. The phalangeal formulae of the manus and pes are unreduced, 2-3-4-5-3 and 2-3-4-5-4, respectively. Total tooth loci in upper jaw of holotype 67, of which 9 in premaxilla; total mandibular tooth loci 62. A single pair of crescentic cloacal bones is present in the holotype and in all male paratypes. In all female paratypes the extent of the intracranial endolymphatic system is made visible in x-rays by its radio-opaque calcium content. The smallest specimen in the type series, AMS R161285, has the epiphyses of the long bones unfused, indicating that is not yet skeletally mature.

**TABLE 3.** Mensural data for the types of *Mniarogekko jalu* sp. nov. Abbreviations as in Materials and methods. All measurements in mm.

	MNHN 2012.0211		AMS R161224		AMS R161286		AMS R161238		AMS R161287		AMS R161288		AMS R161285		CAS 250858		CAS 250859		
	holotype	paratype	male	paratype	male	paratype	male	paratype	female	paratype									
Sex	male	male							female										
SVL	123.3	137.6	121.8	117.2	126.5	116.2	125.4	103.1	125.4	103.1	122.9	139.5	122.9	139.5	122.9	139.5	122.9	139.5	
ForeaL	14.9	14.3	13.6	13.9	14.0	12.3	13.2	11.8	13.2	11.8	13.8	14.5	13.8	14.5	13.8	14.5	13.8	14.5	
CrusL	19.0	19.0	17.8	17.3	18.7	18.9	17.1	14.6	17.1	14.6	17.0	19.4	17.0	19.4	17.0	19.4	17.0	19.4	
TailL	76.2(R)	18.8 (B)	70.9(R)	17.8 (B)	17.5 (B)	66.8 (R)	63.6 (R)	81.4 (R)	63.6 (R)	81.4 (R)	62.4 (R)	49.7 (R)							
TailW	7.9	—	9.2	—	—	7.6	7.0	6.7	7.0	6.7	4.6	5.0	4.6	5.0	4.6	5.0	4.6	5.0	
TrunkL	51.9	56.4	48.5	48.9	52.1	52.8	51.7	42.6	51.7	42.6	57.8	65.2	57.8	65.2	57.8	65.2	57.8	65.2	
HeadL	32.4	33.6	32.3	32.2	32.2	30.4	34.6	27.7	34.6	27.7	33.5	35.6	33.5	35.6	33.5	35.6	33.5	35.6	
HeadW	22.8	24.4	22.7	21.4	23.0	21.7	21.9	20.6	21.9	20.6	22.4	22.6	22.4	22.6	22.4	22.6	22.4	22.6	
OrbD	7.0	7.6	7.0	7.4	7.2	6.6	7.6	6.8	7.6	6.8	7.2	7.8	7.2	7.8	7.2	7.8	7.2	7.8	
EyeEar	10.6	12.4	9.7	10.3	10.8	10.4	10.0	8.3	10.0	8.3	9.0	10.5	9.0	10.5	9.0	10.5	9.0	10.5	
SnEye	12.6	13.9	12.9	12.6	13.5	12.3	13.7	11.3	13.7	11.3	13.0	13.7	13.0	13.7	13.0	13.7	13.0	13.7	
NarEye	9.7	9.7	9.2	8.8	9.1	8.6	9.5	8.0	9.5	8.0	9.3	9.8	9.3	9.8	9.3	9.8	9.3	9.8	
Interorb	15.2	13.5	14.0	13.4	13.7	13.2	13.2	13.6	13.2	13.6	12.9	13.5	12.9	13.5	12.9	13.5	12.9	13.5	
EarL	3.1	3.1	3.5	3.4	2.4	2.4	3.2	1.9	3.2	1.9	4.0	3.2	4.0	3.2	4.0	3.2	4.0	3.2	
Internar	4.8	4.7	4.6	4.6	4.9	3.5	4.0	4.1	4.0	4.1	3.6	4.4	3.6	4.4	3.6	4.4	3.6	4.4	
SupraL L/R	14(10)/12(10)	12(9)/13(10)	13(10)/14(10)	11(8)/10(8)	13(10)/11(10)	13(10)/15(11)	14(12)/13(10)	13(10)/12(10)	14(12)/13(10)	13(10)/12(10)	14(11)/14(9)	13(10)/13(10)	14(11)/13(10)	14(9)	13(10)	14(11)/13(10)	13(10)	13(10)	
InfraL L/R	13/12	12/11	15/13	13/12	13/12	14/13	13/14	13/12	13/14	13/12	12/13	12/12	12/13	12/12	12/13	12/12	12/13	12/12	
LamManus L/R	12-18-20-19-17/13-16-17-14	13-13-16-17-1/3-12-14-15-15-14	13-16-14-16-1/6-12-16-13-17-16	11-17-15-17-1/6-14-17-15-17-13	12-13-17-13-1/0-11-15-17-15-14	13-17-16-17-1/7-13-17-18-18-16	14-17-20-19-1/6-10-17-21-18-18	14-17-17-17-1/6-12-16-17-16-17	14-17-17-17-1/6-12-16-17-16-17	14-17-17-17-1/6-12-16-17-16-17	15-18-21-2/2-20-15-18-20-21-20	14-19-19-1/8-17-14-19-20-9*-18	14-19-19-1/8-17-14-19-20-9*-18	15-18-21-2/2-20-15-18-20-21-20	15-18-21-2/2-20-15-18-20-21-20	15-18-21-2/2-20-15-18-20-21-20	14-19-19-1/8-17-14-19-20-9*-18	14-19-19-1/8-17-14-19-20-9*-18	14-19-19-1/8-17-14-19-20-9*-18
LamPes L/R	13-16-19-19-15/12-18-16-18-15	9-13-14-16-15/10-12-14-17-14	13-15-15-18-16/13-16-17-18-17	11-14-18-20-17/11-14-16-19-17	10-13-17-13-10/11-15-13-18-14	13-15-16-18-16/13-16-19-20-17	13-19-18-20-18/12-16-18-18-18	12-15-16-20-18/15-14-16-20-16	12-15-16-20-18/15-14-16-20-16	12-15-16-20-18/15-14-16-20-16	15-17-15-1/9-18-15-17-23-21-17	14-15-17-1/9-18-13-21-18-9*-17	14-15-17-1/9-18-13-21-18-9*-17	15-17-15-1/9-18-15-17-23-21-17	15-17-15-1/9-18-15-17-23-21-17	15-17-15-1/9-18-15-17-23-21-17	14-15-17-1/9-18-13-21-18-9*-17	14-15-17-1/9-18-13-21-18-9*-17	14-15-17-1/9-18-13-21-18-9*-17
PrecP	21 + 20 17 + 18	17 + 19 13 + 18 4 + 0	18 + 21 19 + 21 6 + 6	17 + 16 16 + 17 3 + 3	13 + 12 11 + 16 1 + 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—

**Variation.** Comparative mensural data for the holotype and paratypes are given in Table 3. Meristic characters of paratypes are mostly similar to those of the holotype, and are mentioned hereafter only if they differ. Postmentals and anterior chin shields highly heterogeneous in many specimens; first infralabials separated to broadly contacting behind the mental.

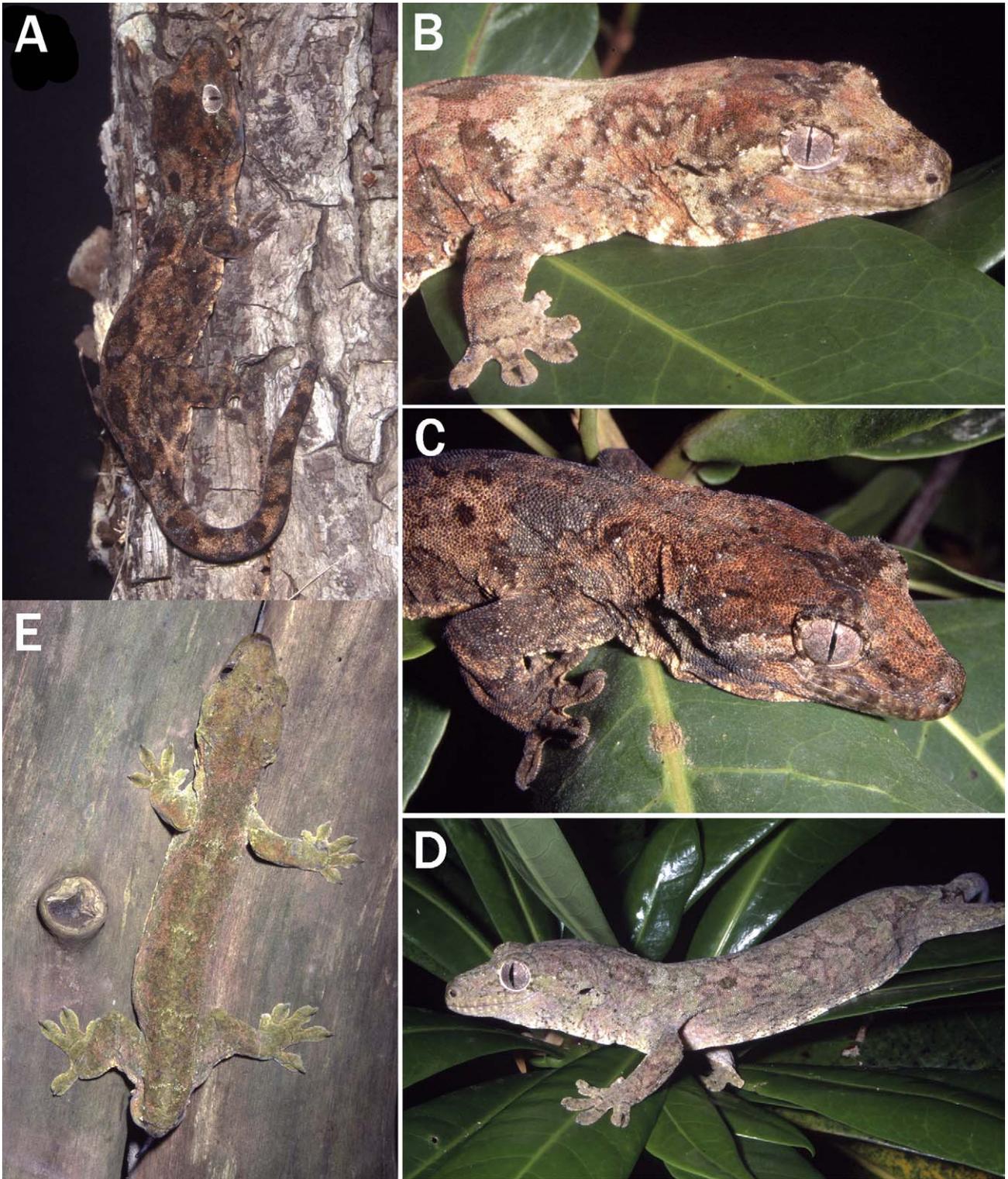
Female specimens lack preloacal pores. All four male paratypes with three rows of preloacal pores, posteriormost much shorter than anterior two.

Color pattern is highly variable across the type series (Fig. 21), from pale grayish to dark brown, but always with dorsal mottling. A darkish patch on occiput, nape, or shoulders usually present. Dorsal patterning diffuse to bold (AMS R161238, 161285, 161288). White scales invariably present, scattered over body; variably expressed but most evident on posterior of head and nape and on shoulders or near forelimb insertions. AMS R16185, which has a largely original tail exhibits irregular caudal banding, with some bands incomplete. Venter variably marked but always with brown mottling, some with distinct, irregular transverse bars or chevrons (AMS R161237, 161286, 161287).

In life the dorsal coloration is a complex and often irregular pattern of several different colors, including grayish brown, brick red, salmon, and mossy green (Fig. 21). There is typically a white or lichenous green nape patch and the mid-dorsum typically bears a series of dark blotches with lighter centers. The flanks and side of the head bear scattered small white flecks. A dark reddish brown, posteriorly-directed triangle is usually present on the fronto-parietal region of the head. The original tail bears irregular dark blotches on a reddish brown background. The venter from the posterior portion of the throat to the pygal portion of the tail is a pale yellowish-green with diffuse chevrons or transverse bands of brown (Fig. 20). The anterior portion of the throat is white with dark brown transverse markings, some fusing to form broad swaths of dark pigment, or it may be entirely brown. The iris is silvery and the tongue and mouth lining are unpigmented. Although it is unclear if there are consistent geographical differences in coloration, specimens from Forêt d'Ougne and Néhoué appear greener than those from Île Art and Tiébaghi.



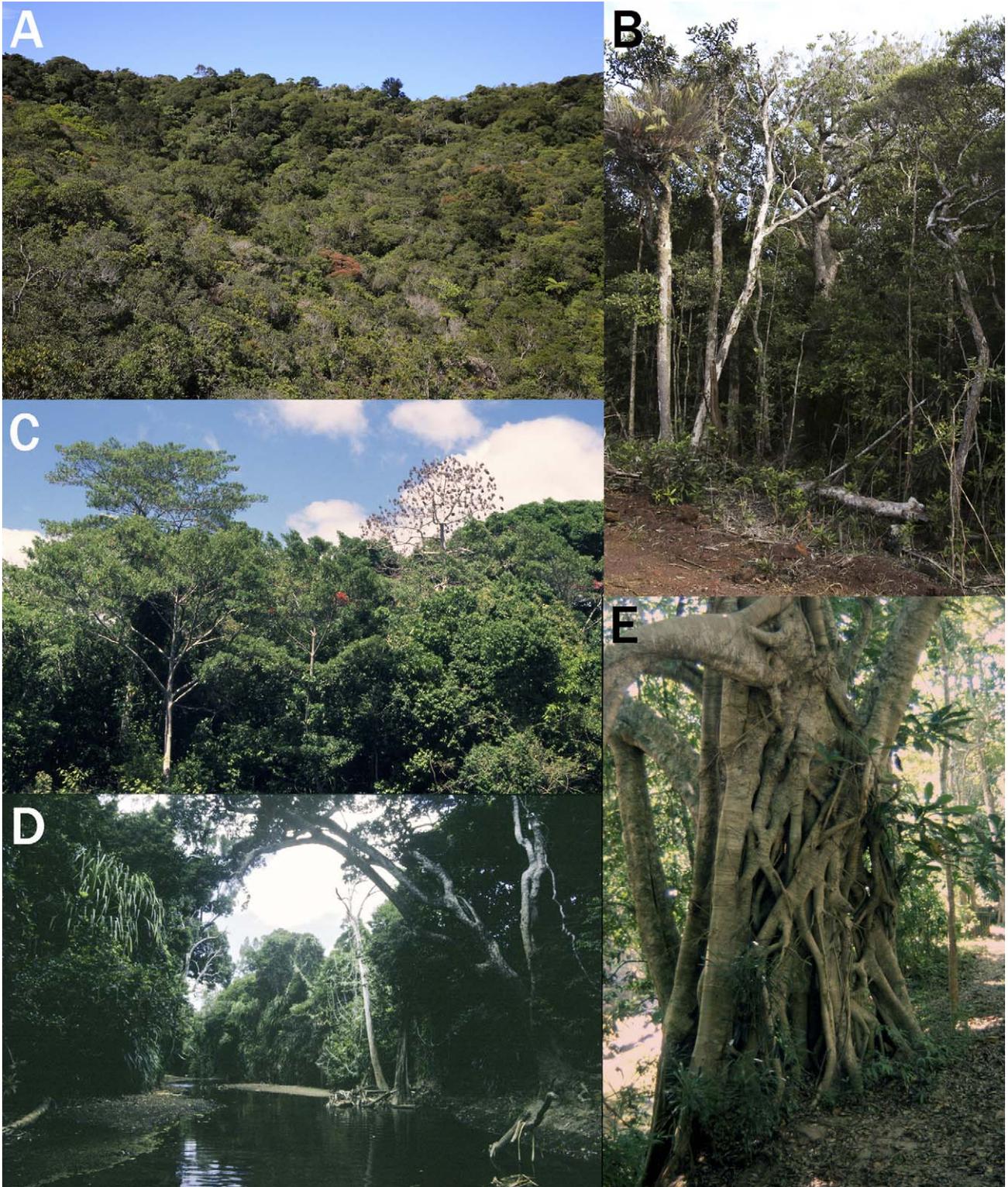
**FIGURE 20.** Ventral view of freshly euthanized specimens of *Mniarogekko jalu* sp. nov. from Île Art, Îles Belep showing the heavily patterned venter with greenish-yellow tinge. From left to right: holotype (MNHN 2012.0211), paratypes (AMS R161286, AMS R161287, AMS R161288). Photo by A.H. Whitaker.



**FIGURE 21.** Life photographs of *Mniarogekko jalu* sp. nov. from Île Art, Îles Belep (A, B), Dôme de Tiébaghi (C), Rivière Néhoué (D), and Forêt d'Ougne, Vallée Poupoule (E). Photos by A.H. Whitaker.

**Etymology.** The specific epithet is derived from the word *jâlu*, which means spirit (a being from the spirit world) in the Nyêlâyü language which is used in the northern Province Nord from Balade, through Ouégoa, Baie de Harcourt to Arama, and on Balabio and the Îles Belep. The name is thus parallel in construction to that of its sister taxon *M. chahoua*, which according to Bavay (1869) meant “devil” in an unspecified Kanak language. Throughout New Caledonia giant geckos have an association with elements of the spirit world that are both feared and respected (Bauer & Sadlier 2000). The name is a noun in apposition.

**Distribution.** The first confirmed record of *Mniarogekko jalu* was at Rivière Néhoué in 1998 (Siepp & Henkel 2000; Henkel & Böhme 2001) and it was subsequently illustrated by Watkins-Colwell (2003) and Langner (2009). Since then *M. jalu* has been recorded at two further locations in the extreme north of Grande Terre (Dôme de Tiébaghi and Forêt d'Ougne) and from Île Art in the Îles Belep, 40 km north of the Grande Terre, and its continued occurrence Rivière Nehoué has been confirmed (Whitaker *et al.* 2004; Langner 2009; Fig. 17).



**FIGURE 22.** Habitats of *Mniarogekko jalu* **sp. nov.** at the Dôme de Tiébaghi (A, B), Forêt d'Ougne, Vallée Poupoule (C), and Rivière Néhoué (D, E). Photos by A.H. Whitaker.

**Natural History.** *Mniarogekko jalu* has been found only in old-growth, closed-forest habitat with large canopy trees. These typically have numerous holes, cracks and crevices which would provide an array of sheltering sites by day. The Rivière Néhoué (Fig. 22D–E) and Forêt d’Ougne (Fig. 22C) localities are at low elevation (<10 m) on schist substrates, with the geckos inhabiting tall gallery forests (to more than 20 m) on alluvial soils along the valley floors. The Dôme de Tiébaghi (Fig. 22A–B) and Îles Belep (Fig. 16) localities are on ultramafic substrates—at Dôme de Tiébaghi one population is in mid-elevation (280–380 m) gully forest with a canopy height to about 12 m; on the summit plateau of Dôme de Tiébaghi (500–550 m) and the plateaux of Île Art (220–250 m) the geckos inhabit low (<8 m) closed forest on bouldery cuirasse surfaces.

*Mniarogekko jalu* appears to be exclusively arboreal. At night they have been observed foraging in the twigs and outer foliage of canopy trees or less often perched on branches and trunks in the upper vegetation strata (all observations of this species made at night were in the upper half of the vegetation). During the day they shelter in crevices and holes in branches and trunks, often descending close to the forest floor (<1 m) to such sites. Favored retreat sites are in the holes and crevices in the complex root structure of banyan trees (*Ficus prolixa* G. Forst., Fam. Moraceae). When in retreat crevices this species often rests near the entrance where it is clearly visible, only moving out of sight when disturbed. Eggs of *M. jalu* were found in a tree crevice 2.5 m above the ground on Dôme de Tiébaghi and in humus in epiphytic ferns 8 m above ground at Forêt d’Ougne (AMS R161280). Paratype CAS 250858, collected in late January at Rivière Néhoué, has two large eggs visible in x-ray.

At Forêt d’Ougne this species was frequently observed at night in the emergent crowns of cerisier bleu trees (*Elaeocarpus angustifolius* Blume, Fam. Elaeocarpaceae) that were fruiting heavily and, as the sister species *M. chahoua* is known to be at least partially frugivorous (Bauer 1985), were assumed to be feeding on the fleshy berries.

The defence behaviour of *R. jalu* when under immediate threat was to take evasive action by coiling into a tight ball and falling from the vegetation to the forest floor. This evasive behaviour has also been documented in captive *M. chahoua* (Vosjoli *et al.* 2003).

Trombiculid mites are present between lamellae and in one or both popliteal pockets in all of the specimens examined. In one specimen mite infestation of the cloacal sacs is extreme and mites have caused and/or infested a midventral cavity between the cloacal sac apertures.

On Île Art *Mniarogekko jalu* is syntopic with *Correlophus belepensis*, *Eurydactylodes agricolae* and *Dierogekko insularis* and at Dôme de Tiébaghi it is syntopic with *Rhacodactylus auriculatus*, *Eurydactylodes agricolae* and *Dierogekko nehoueensis*. At the other two locations it is the only giant gecko species present but is variously syntopic with *Bavayia* aff. *exsuccida*, *B.* aff. *cyclura*, *Eurydactylodes agricolae* and *Dierogekko nehoueensis*. Other sympatric lizards in its habitat include *Hemidactylus frenatus*, *H. garnotii* Duméril & Bibron, 1836, *Lepidodactylus lugubris*, *Caledoniscincus aquilonius* Sadlier, Bauer & Colgan, 1999, *C. atropunctatus*, *C. austrocaledonicus*, *C. haplorhinus*, *Kanakysaurus viviparus*, *Lioscincus nigrofasciolatus*, *L. novaecaledoniae* (Parker, 1926) and *Phoboscincus garnieri*.

**Conservation status.** At present *Mniarogekko jalu* is known only from a small part of northern Grande Terre, north of Koumac, and on the Belep archipelago. Whether its actual range is so confined is unclear but the nearest known location for its sister species *M. chahoua* is at Vallée d’Amoa, on the east coast 105 km south-east of Koumac (Bauer & Sadlier 2000). Within the known extent of occurrence for *M. jalu* the old-growth closed forests that are its preferred habitat are now reduced to scarce and isolated remnants—largely as a result of repeated burning since the arrival of Melanesian colonists >3000 ybp but also including more recent clearance for cattle ranching and, in localized areas, for mining.

*Mniarogekko jalu* faces a number of direct and indirect threats. All remaining areas of forest habitat are under continued threat from wildfires that affect northern New Caledonia each dry season. Browsing ungulates are fortunately absent from the Îles Belep but the forests on the Grande Terre suffer the on-going depredations of Sunda Sambar, *Rusa timorensis* (de Blainville, 1822), and feral pigs at all localities, with the addition of cattle at Rivière Néhoué and Forêt d’Ougne. Introduced rats (*Rattus* spp.), feral cats and little red fire ants (*Wasmannia auropunctata*) are present at all localities where *M. jalu* has been found. Rats and cats are known to be serious predators of lizards but no direct evidence of predation on *M. jalu* was obtained; little red fire ants are known to have a severe impact on lizard populations, even resulting in local extirpation (Jourdan *et al.* 2000, 2001).

The localities on Dôme de Tiébaghi are under immediate threat of total destruction resulting from expansion of the open-cast nickel mine on the massif. Although there appear to be no immediate plans to mine on Île Art, the

ultramafic plateaux have had extensive prospecting for nickel in the past and the whole area is held under current mining licenses. The Forêt d'Ougne locality is on a cattle ranch and subject to on-going browsing pressure. Only the locality at Rivière Néhoué has reserve status. However, it is administered as a recreation reserve, is small in extent and has high human use.

There are no quantitative data on population size and trends available for *Mniarogekko jalu*. Surveys in 2001–2002 indicated that it was relatively numerous at each of the known sites, with encounter rates ranging from 0.19/hour on Dôme de Tiébaghi to 1.75/hour on Île Art, and at Forêt d'Ougne eight were observed on 190 m of forest margin (Whitaker *et al.* 2004). However, two factors point to the species' potential vulnerability. In 2001 at Forêt d'Ougne *M. jalu* was relatively common in one valley yet it was not detected in an immediately adjacent valley (<350 m away) with identical forest but where little red fire ants were exceptionally abundant. Also in 2001 *M. jalu* was moderately abundant in closed forest at a gully site on the slopes of Dôme de Tiébaghi but it could not be detected at this same location six years later after increased mining activity had led to the vegetation being blanketed in wind-blown dust from a nearby mining haul-road.

Because of its limited extent of occurrence, restricted area of occupation (<30 km<sup>2</sup>), limited number of locations (four), the threats to its habitat (wildfires, browsing ungulates, mining), the presence of mammalian predators (rats, cats) and the impacts of fire ants, *Mniarogekko jalu* is assessed as Endangered (B1a, b[ii–iii, v]; B2a, b[ii–iii, v]) (IUCN 2001).

**Remarks.** *Correlophus ciliatus* x *Mniarogekko chahoua* hybrids have been reported in captivity (Seipp & Henkel 2011), thus, despite their genetic divergence, it is likely that there is also some degree of compatibility between members of the two genera. Indeed, levels of genetic differentiation between genera of New Caledonian diplodactylids are relatively low in comparison to many other gecko groups (Jackman & Bauer 2006), so it is not surprising that similarly-sized members of the clade can interbreed. Although the viability of F1 hybrids has been demonstrated, we are unaware of data on their fertility or the viability of subsequent generations.

Jouan (1863, 1864) noted the existence of a giant gecko on the Îles Belep, but collected no specimens. As *Rhacodactylus* spp. appear to be absent from this island group, it seems likely that Jouan's reports refer to *M. jalu*, which is the largest gecko on the Belep islands and is relatively abundant in appropriate habitat (Whitaker *et al.* 2004).

## Discussion

The non-monophyly of the long-recognized New Caledonian diplodactylid genera *Bavayia* and *Rhacodactylus* was first suggested by Bauer *et al.* (2004) and Bauer and Jackman (2006). On the one hand, the former group represented species sharing a suite of plesiomorphic features and characterized as being small with a very generalized in body form (no tubercles, skin flaps, or ornamentation). *Rhacodactylus* species, on the other hand, were grouped on the basis of a single, presumably apomorphic character, large body size, despite obvious morphological differences among the constituent species. Although further nuclear data would be desirable in order to assess relationships within the New Caledonian clade, we believe that our ND2-dominated dataset gives the best approximation of the natural groupings of species previously included in this genus. The case for the non-monophyly of *Rhacodactylus* rests on the sister-group relationship between *Eurydactylodes* and *Mniarogekko* as well as the apparent distinctness of the species of *Correlophus* relative to other large-bodied taxa.

In recent years the interpretation of the New Caledonian herpetofauna has changed dramatically. In keeping with then prevailing views regarding the geological history of New Caledonia and the antiquity of its biota, Bauer (1990, 1995) and Bauer and Sadlier (1993, 2000) regarded diplodactylids to be of possible Gondwanan origin. More recent geological interpretations of the region suggest that New Caledonia was submerged in the early Paleogene, at least until the Mid- to Late Eocene (Cluzel *et al.* 2001; Murienne *et al.* 2005; Pelletier 2006; Ladiges & Cantrill 2007). This is consistent with dating estimates derived from molecular phylogenies of a diversity of lineages that suggest intra-New Caledonian cladogenesis has taken place in the last 37 million years (Grandcolas *et al.* 2008). Data from both skinks (Smith *et al.* 2007; Chapple *et al.* 2009) and diplodactylid geckos (Bauer *et al.* 2004, 2006b; Oliver & Sanders 2009; Nielsen *et al.* 2011) support probable Early to Mid-Miocene basal cladogenesis within New Caledonian crown clades, with the most recent speciation events probably no older than 5–6 Ma. This implies that cladogenetic events throughout the Mid- to Late Tertiary may have played a role in the

fragmentation and speciation of the New Caledonian lizard fauna. In addition to a variety of candidate geological events, there were significant climatic and vegetation changes in New Caledonia during this period (Lowry 1998; Lee *et al.* 2001) and these may be relevant to herpetofaunal diversification, although specific candidate cladogenetic events remain elusive. We have not explicitly investigated the timing of lineage splits in the giant geckos of New Caledonia in this paper, however, Skipwith (2011) has corroborated earlier estimates that the primary diversification of these and other New Caledonian gecko lineages occurred in the Miocene. Further research on the divergence dating of the New Caledonian diplodactylids is ongoing (Skipwith, Jackman & Bauer, unpublished).

Perhaps the overriding outcome of the last decade of herpetological research in New Caledonia has been the degree of microendemism that has been revealed (Bauer & Jackman 2006; Bauer *et al.* 2006b; Sadlier *et al.* 2009). This has, in part been the result of the application of molecular phylogenetic techniques that have identified cryptic taxa. However, it has also been the result of a concerted field effort that has yielded collections from more and more localities around New Caledonia. Much of the increase in recognized lizard diversity has been the outcome of recent explorations of the ultramafic massifs and adjacent regions of northwestern New Caledonia (e.g., Whitaker *et al.* 2004). Such substrates are known for their association with lineage diversification in other biotic groups (Espeland *et al.* 2008; Espeland & Johanson 2010) and among reptiles they have yielded the discovery and description of the entirely novel genera *Kanakysaurus* (Sadlier *et al.* 2004) and *Oedodera* (Bauer *et al.* 2006a), the recognition of *Dierogekko* as a genus distinct from *Bavayia* (Bauer *et al.* 2006b), and the description of many new species in a diversity of genera (Sadlier, Bauer, Whitaker & Smith 2004; Sadlier, Smith, Bauer & Whitaker 2004; Bauer *et al.* 2006b, Sadlier *et al.*, 2009).

The two giant geckos described herein are both limited to the far north of New Caledonia. *Mniarogekko jalu* occurs at a number of localities that represent areas of endemism for other lizards, such as the Rivière Néhoué/Dôme de Tiébaghi region. It also occurs on the Îles Belep, along with *Correlophus belepensis*, which appears at present to be restricted to those islands. This latter species is the first lizard endemic to this island group, although *Dierogekko insularis* occurs only on the Îles Belep and the nearby Île Yandé. This further highlights the extent of narrow range endemism seen in the New Caledonian herpetofauna, which is also underscored by the formal resurrection of *Rhacodactylus trachycephalus* from the synonymy of *R. trachyrhynchus*. Although we have documented *R. trachycephalus* with certainty only on a tiny coralline island off Île des Pins, it is possible that it also occurs on the Île des Pins, another recognized area of lizard endemism (Börner 1980; Sadlier *et al.* 2006), a situation that may also apply to the recently rediscovered *Phoboscincus bocourti* (Ineich 2009).

These examples highlight the need for conservation measures on a fine scale in New Caledonia, particularly on vulnerable offshore islands. Such small, localized populations are at particular risk from introduced predators, which are widespread in New Caledonia (Gargomigny *et al.* 1996). Further, giant geckos are known to be popular in the pet trade. Although some species are bred in captivity quite cheaply and in great numbers, the live-bearing *Rhacodactylus trachycephalus* remains commercially expensive and may, like the two new species, at least one of which has not entered the pet trade (*M. jalu* may already be traded, either as pure stock or in lineages including *M. chahoua* and *M. jalu* crosses), be at risk to illegal collection and export. While skinks are less in demand in the pet trade than geckos, *Phoboscincus bocourti* might well also be at risk.

On this basis we strongly recommend an assessment of the particular conservation requirements of these offshore islands, on which these lizards are totally reliant, in order that some minimum level of legal protection can be afforded to these large, biologically intriguing, and charismatic reptiles. We also recommend an assessment of the status of populations of *Correlophus belepensis* on the Tolé Munu and Kalidan plateaux on Île Art be undertaken as these sites appear to be crucial for this species, as well a diversity of other lizards, including good populations of the northern endemics *Dierogekko insularis*, *Mniarogekko jalu* **sp. nov.**, and *Eurydactylodes agricolae*. They also have a number of endemic plant species, some of which are very rare (Butin 2009; Munzinger *et al.* 2009), and very likely support endemic invertebrates. Most of the remaining area of the Belep islands is dominated by degraded shrublands that result from repeated wildfires and clearance for gardening and, in the case of Île Dau Âc, Île Aafa and Île Caafa, from feral goats (Butin 2009). Because browsing mammals are not established on Île Art the forests of the Tolé Munu and Kalidan plateaux represent the most pristine habitat remaining (Butin 2009; Munzinger *et al.* 2009; Whitaker *et al.* 2004). Despite the presence of rats, feral cats and little red fire ants, and the effects of past mineral exploration and on-going limited cutting of timber for local use, these forests are essential for the conservation of threatened lizard species.

In the south we recommend that local authorities establish the entirety of Îlot Môrô as a reserve. Môrô has one of the most diverse combinations of habitats of the offshore islands in the vicinity of the Île des Pins (Geneva 2007). The island supports the only verified population of the critically endangered *Rhacodactylus trachycephalus* as well as a large population of *R. leachianus* (Cunkelman 2005). Môrô also harbors a large number of wedge-tailed shearwaters *Puffinus pacificus* (Gmelin) and its central forest, in a partially flooded depression, is unique among the southern satellite islands. A similar consideration should be given to the larger Îlot Brosse, which supports the only known extant population of the recently rediscovered *Phoboscincus bocourti* (Bauer & Sadlier 2000; Geneva 2007; Ineich 2009) as well as *R. leachianus* (Seipp & Henkel 2000). Brosse is a much larger island than Môrô and more remote from the Île des Pins, but both islands are frequently visited. Îlot Môrô, in particular is a popular picnic spot and may be reached in only minutes from Kuto. These southern islands are at particular risk from both invasive animals and illegal collection as they are easily visited and locals are familiar with seeing tourists and other strangers in the area, whereas the Îles Belep are generally not visited by outsiders and are also more difficult to access.

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## APPENDIX

Specimens of New Caledonian Giant Geckos (exclusive of *Correlophus belepensis* **sp. nov.** and *Mniarogekko jalu* **sp. nov.**, for which see text). All specimens are from New Caledonia. All specimens have been examined by one or more of the authors except for those indicated by an asterisk (\*). Maps are based on these vouchered specimens plus selected literature and sight records listed below each species specimen lists. Coordinates for AMB, AMS and CAS specimens recorded using a GPS or derived from topographic maps by the collectors. For most other records

coordinates have been estimated based on the stated specimen locality and the authors' familiarity with suitable habitat. Records too general to map are listed without coordinates.

*Correlophus ciliatus*:

PROVINCE NORD: Canala (21°31'40"S, 165°37'45"E): MNHN 6475. PROVINCE SUD: Mt. Dzumac (22°02'S, 166°27'E): AMS R150736; Rivière Bleue, vic. Pont Germain (22°06'S, 166°38'E): AMS R146594–95, 153461; CAS 205458, 205482; Rivière Bleue, vic. Pont Germain (22°06'S, 166°39'E): AMS R147971; Rivière Bleue, vic. Pont Germain (22°06'02"S, 166°39'30"E): AMS R152608; Nouméa (22°15'50"S, 166°27'10"E): MNHN 4213; Île des Pins (no precise locality): BYU H46319, SMF 89432, ZSM 853/2001. NEW CALEDONIA (no precise locality): AMB 5266, BMNH 85.11.16.5–6, 85.11.16.7, 90.7.26.2–3a,3b, IRSNB 797, 797β, MCZ R183419; MNHN 701 (**paralectotype**), 701a (**lectotype**), 1312, 1755, 1974.802, MVZ 230111–12; NMW 17927(1–2), YPM 9887, 10206, 11896, 13360, 13477, 13554; 16086, 16211–13, ZSM 892/2001, 900/2001, 927/2001, 148/2003.

ADDITIONAL UNVOUCHERED RECORDS MAPPED. PROVINCE SUD: Pourina River Valley (22°01'45"S, 166°43'30"E): Ekstrom *et al.* (2000); près du Lac de Yaté (22°10'S, 166°50'E): Girard & Heuclin (1998); Mt. Koghis (22°10'38.5"S, 166°30'34.6"E): A.H. Whitaker sight record; Kucaartüü, Île des Pins (22°35'10.7"S, 167°31'14.5"E): A.H. Whitaker sight record.

*Correlophus sarasinorum*:

PROVINCE SUD: Rivière Bleue, vic. Pont Germain (22°06'S, 166°38'E): AMS R146596; Rivière Bleue Forest Reserve (22°06'S, 166°39'E): AMS R127440–41; Rivière Bleue, vic. Giant Kauri (22°06'S, 166°39'E): AMS R145525; Col de Yaté (22°09'47"S, 166°54'42"E): AMS R166127; Le Bois de Sud (22°10'22"S, 166°45'53"E): AMS R161920–21; Mt. Koghis (22°10'43"S, 166°30'20"E): AMS R90188, R150764, R152657–58; CAS 202723, 202747, 205421–22; 1 km S Touaourou (22°13'15"S, 166°59'02"E): CAS 157675; 20 km S Nouméa (22°14'00"S, 166°37'00"E): ZFMK 46408, 49284–86, 51821, 55032–39; Pic du Pin (22°14'53"S, 166°49'45"E): AMS R164255, 164286; Route de la Goro/Route de la Mine intersection (22°14'53"S, 166°49'45"E): AMS R166125; Goro Plateau, Wadjana river drainage, barrage (22°16'25.2"S, 166°59'21.8"E): AMS R179047; Goro Plateau, Kwe Nord Range (22°16'47.0"S, 166°56'46.2"E): AMS R172142; Goro Plateau, Wadjana river drainage, barrage (22°17'30.3"S, 167°00'06.1"E): AMS R179046; Pic du Grand Kauri (22°18'17"S, 166°57'39"E): AMS R166051; Plaine des Lacs, Kwa Néie (22°18'55"S, 166°54'47"E): AMS R150019–23; Prony (22°19'25"S, 166°49'07"E): NMBA 7246 (**holotype**); Plaine des Lacs, Forêt Nord on SW base of Kwa Néie (22°19'28"S, 166°54'51"E): AMS R150030, 162987, 165977–78, 166077–78. NEW CALEDONIA (without precise locality): MNHN 94.452 (**paratype**), YPM 9901, ZSM 810/1997, 57/1999.

ADDITIONAL UNVOUCHERED RECORDS MAPPED. PROVINCE SUD: Col de la Pirogues (22°14'40"S, 166°39'53"E): J. le Breton photograph.

*Mniarogekko chahoua*:

PROVINCE NORD: 0.5 km W of Rte 3 on Vallée' d' Amoa Rd, ca 3.3 km N of Poindimié (20°54'50"S, 165°17'32"E): CAS 162177; 1.0 km W of Rte 3 on Vallée' d' Amoa Rd, ca 3.3 km N of Poindimié (20°55'02"S, 165°17'22"E): CAS 167764; St. Therese, 15 km NE Poindimié, Vallée d' Amoa (20°58'00"S, 165°13'20"E): CAS 156691–92 (**neotype**); Coula, zwischen Bourail und Houaïlou (21°20'30"S, 165°27'00"E): SMF 61779, 61780–81 (captive born); Kanala, Lifou [sic! Canala] (21°31'40"S, 165°37'45"E): EMNB\* [lost] (**holotype**). PROVINCE SUD: Sarraméa (21°38'S, 165°50'E): AMS R144171; La Foa (21°42'00"S, 165°50'00"E): ZFMK 27653, 30549, 38631–34, 42410, 45382–83, 49285; Mt. Koghis (22°10'45"S, 166°30'15"E): SMF 89415. NEW CALEDONIA (no precise locality): AMB 5272, NMBA 9702, YPM 13546, 16068–69.

ADDITIONAL UNVOUCHERED RECORDS MAPPED: Île des Pins (no precise locality): (Seipp & Henkel 2000).

*Rhacodactylus auriculatus*:

PROVINCE NORD: Dôme de Tiébaghi, 14 km NW Koumac (20°27'38"S, 164°11'11"E) AMS R161250–253; Mt. Kaala, 6 km N Kaala-Gomen, headwaters of Oué Injob (20°37'03"S, 164°22'49"E): AMS 161093–94; Massif de Koniambo, 8 km NE Koné, headwaters of Rivière Pandanus (20°59'51"S, 164°48'47"E): AMS R161116–19; Massif Kopéto (21°10'S, 165°01'E): AMS R163101–02, 163129–30; Plateau de Tia, S Pouembout (21°10'57"S, 164°53'04"E): AMS R163166–67; Massif du Boulinda, 1.5 km SW Mt. Boulinda (21°15'51"S, 165°08'28"E):

AMS R163182; Massif du Boulinda, 2 km SW Mt. Boulinda (21°16'34"S, 165°08'09"E): AMS R163193; Vitôrhué, 0.5 km NW Mé Mwa, Ménazi Massif (21°25'53.7"S, 165°44'21.9"E): AMS R179902; Mé Pwêida, 2 km NW Gwâ Rùvianô, Ménazi Massif (21°26'07.0"S, 165°40'58.1"E): AMS R179900–01; 0.6 km NW Bwa Méyu (21°29'15"S, 165°52'02"E): AMS R167471. PROVINCE SUD: Umgebung Thio (21°37'00"S, 166°13'00"E): NMBA 7048; Vallée de la Nimbo (21°42'49"S, 166°22'28"E): MNHN 1985.109; Pic Ningua (21°43'27"S, 166°08'12"E): AMS R171233; Pic Ningua (21°44'25"S, 166°09'21"E): CAS 250856–57; Pic Ningua (21°44'31"S, 166°09'20"E): AMS R171242; Pic Ningua (21°44'36"S, 166°09'02"E): CAS 250854–55; 1.3 km from summit of Mt. Do (21°45'35"S, 165°59'48"E): AMS R146446; 2.2 km from summit of Mt. Do (21°46'S, 166°00'E): AMS R146448, CAS 198778; 2.6 km from summit of Mt. Do (21°46'00"S, 166°00'15"E): AMS R146447, CAS 198779; Ngoi Tal (21°49'40"S, 166°27'30"E): NMBA 7047; Kouakoué (21°57'00"S, 166°31'00"E): BMNH 1926.9.17.5; Mt. Ouin (22°01'10"S, 166°28'18"E): CAS 250848; Pic Ningua (22°01'25"S, 166°28'12"E): CAS 250846–47; ridge between Mt. Ouin summit and Mt. Dzumac (22°00'57"S, 166°28'03"E): AMS R165791–92; CAS 202829, USNM 515883.6264345; Mt. Dzumac (22°02'S, 166°27'E): AMS R150735; Mt. Dzumac (22°02'30"S, 166°27'10"E): ZFMK 29111; Vallée de la Ouinné (22°02'03"S, 166°29'31"E): MNHN 1985.108; Rivière Bleue, vic. Panoramique (22°05'44"S, 166°40'07"E): CAS 205461; Rivière Bleue, vic. Pont Germain (22°06'S, 166°39'E): Rivière Bleue, vic. Giant Kauri (22°06'S, 166°40'E): AMS R135182–83, R146593; AMS R147369, R147961–70, R147980; Rivière Bleue, Refuge, vic. Pont Germain (22°06'02"S, 166°38'41"E): AMS R152625–26; Rivière Bleue, vic. Pont Germain (22°06'02"S, 166°39'30"E): AMS R152606–07, R152634–35; Rivière Bleue, vic. Pont Germain (22°06'10"S, 166°39'10"E): CAS 205429–38, 205475–76; Rivière Bleue, 0.5 km S Pont Germain (22°06'10"S, 166°39'30"E): CAS 202837; Montagne des Sources (22°07'36"S, 166°36'17.4"): MCZ A27378–79; Mt. Gouémba (= Wô Bwa Wîwâ), 4km up Mt. Gouémba Rd. (22°09'S, 166°54'E): AMS R78113–25; Yaté (22°09'30"S, 166°54'12"E): NMBA 7050–51; Yaté: CAS 157684 (22°09'30"S, 166°55'30"E); Mt. Gouémba (= Wô Bwa Wîwâ) (22°10'00"S, 166°56'27"E): CAS 250849–53; Mt. Gouémba (= Wô Bwa Wîwâ), 3km S La Fausse Yaté Bridge (22°10'S, 166°57'E): AMS R78126–27; Mt. Koghis (22°10'43"S, 166°30'20"E): AMS R78334–38; Touaourou, 1 km S (22°11'57"S, 166°58'30"E): CAS 157681; Touaourou, 2 km N Gite St. Gabriel (22°12'15"S, 166°58'45"E): CAS 15825; 20 km S St. Louis (22°12'25"S, 166°41'50"E): CAS 165859; Goro Plateau, Plaine des Lacs (22°12'50"S, 166°56'50"E): AMS R179069–73; Goro, 12 km NW Gite Wadiana (22°13'10"S, 166°59'20"E): CAS 158922; Touaourou, 1 km S Gite St. Gabriel (22°13'20"S, 166°59'20"E): CAS 157679, 157682, 158923, 165891; Goro, 11 km NW Gite Wadiana (22°13'42"S, 166°59'42"E): CAS 158919; Plaine des Lacs, Chutes de la Madelaine (22°13'52"S, 166°51'28"E): AMS R148074–75; 20 km S Nouméa (22°14'00"S, 166°37'00"E): ZFMK 43584, 43685–89, 45036, 45384, 46119; Col des Mourange (22°14'S, 166°40'E): AMS R135197, R146450–52, R146592, CAS 198780–81; Touaourou, 3 km S Gite St. Gabriel (22°14'00"S, 167°00'05"E): CAS 157683; Touaourou, 4 km S Gite St. Gabriel (22°14'40"S, 167°00'07"E): CAS 162183; Route de la Goro/Route de la Mine intersection (22°14'53"S, 166°49'45"E): AMS R166018–19; Plaine des Lacs, 2 km NE Pic du Pin (22°15'S, 166°50'E): AMS R78232–33; Touaourou, 6 km S Gite St. Gabriel (22°15'13"S, 167°00'20"E): CAS 157676, 158920, 162179–81; Touaourou, 5 km S Gite St. Gabriel (22°15'15"S, 167°00'20"E): CAS 157677–78, 162182, 165858, 165892, 165901; Goro, 8 km N Gite Wadiana (22°15'15"S, 167°00'25"E): CAS 157680; Goro Plateau, Plaine des Lacs (22°15'35.4"S, 166°56'52.2"E): AMS R179125–27; Nouméa (22°15'50"S, 166°27'10"E): NMBA 2909; Vicinity Nouméa: BMNH 86.3.11.5–9; Plaine des Lacs, Route de la Wajana (22°16'09"S, 166°57'35"E): AMS R166107; Plaine des Lacs, Route de la Wajana (22°16'19"S, 166°56'24"E): AMS R166106; Goro Plateau, Plaine des Lacs (22°16'23.2"S, 166°57'35.9"E): AMS R179128; Plaine des Lacs, Route de la Wajana (22°16'26"S, 166°58'32"E): AMS R166111; Plaine des Lacs, Route de la Wajana (22°16'26"S, 166°57'43"E): AMS R166003; Goro Plateau, Kwe Nord (22°16'30.0"S, 166°58'06.0"E): AMS R179195, 179292–93; Plaine des Lacs, Route de la Wajana (22°16'34"S, 166°58'55"E): AMS R166176; Goro Plateau, Kwe Nord (22°16'34.5"S, 166°58'06.0"E): AMS R179193–94; Plaine des Lacs, Route de la Wajana (22°16'35"S, 166°58'38"E): AMS R166112–13; Goro Plateau, Baie de Prony (22°16'50.4"S, 166°51'49.7"E): AMS R179094–95, 179105, 179114; Goro Plateau, Baie de Prony (22°16'53.2"S, 166°52'42.4"E): AMS R179115; Mt. Dore (22°17'00"S, 166°35'30"E): EMNB\* [lost] (**holotype**), SMF 89416; Mt. Dore, 2 km W of Plum turnoff (22°17'S, 166°37'E): AIM 926, AMS R78304–08, R90186–87, R93711; Goro Plateau, Kwe Nord (22°17'01.0"S, 166°57'58.9"E): AMS R1791272, 179294; Plaine des Lacs, Route de la Wajana (22°17'04"S, 166°58'57"E): AMS R166025, R166114; Pic du Grand Kaori (22°17'05"S, 166°53'28"E): AMS R164342; Goro Plateau, Koué drainage, Kwe Nord (22°17'14.3"S, 166°54'47.8"E): AMS

R179063, 179068; vicinity Goro (22°17'15"S, 167°00'40"E): CAS 165895–900; Goro Plateau, Koué drainage, Kwe Nord (22°17'21.2"S, 166°54'28.7"E): AMS R179064–67; Goro Plateau, Koué drainage, Kwe Nord (22°17'32.1"S, 166°55'49.1"E): AMS R179060–62; Plaine des Lacs, Route de la Wajana (22°17'35"S, 166°59'33"E): AMS R166173; Bay of Prony near Carenage (22°17'56"S, 166°49'30"E): UMMZ 174094; Goro, 1 km NW Gite Wadiana (22°17'58"S, 167°00'33"E): CAS 158924, 165860; 11 km S Gite St. Gabriel (22°18'05"S, 167°00'30"E): CAS 159512; Pic du Grand Kauri (22°18'17"S, 166°57'39"E): AMS R166054; Goro, Gite Wadiana (22°18'35"S, 167°00'25"E): CAS 158921, 162178, 165902; Plaine des Lacs, Kwa Néie (22°18'55"S, 166°54'47"E): AMS R150007–08, R152645–50, CAS 205484–486; Plaine des Lacs, Forêt Nord (22°18'55"S, 166°54'47"E): AMS R166082–83; Prony (22°19'25"S, 166°49'07"E): MCZ R-15968; Mt. l'Aiguillon (22°21'S, 166°55'E): CAS 158389–90; Cap N'Doua (22°23'08"S, 166°55'44"E): AMS R164313. NEW CALEDONIA (no precise locality): AMB 5267, BMNH 85.11.16.2–4, MCZ R18011, MLI\* [lost], MNHN 5305, 5305a, 86.393–95, 87.272–75, 94.450–51, 1974.804–05, NHMG 874(1–3), 658(1–11), NMW 17926(1–4), 18609, RMNH 5451, ROM 22645, SMF 61778, 64806, 71024, 89413–14, UMMZ 127599, YPM 13895, 17620–21, 17746, ZFMK 38940, ZIN 5402, ZMH R02830, ZSM 300/1988, 346/1988 (2 spec.), 401/1988, 181/1999 (2 spec.), 5/1994, 852/2001, 926/2001.

ADDITIONAL UNVOUCHERED RECORDS MAPPED: PROVINCE NORD: Pointe de Babouillat, Baie de Néhoué, 24 km N Koumac (20°23'18"S, 164°07'53"E): A.H. Whitaker sight record; Ruisseau des Gaiacs, Paagoumène, 6 km, NW Koumac (20°30'56.3"S, 164°14'54.2"E): A.H. Whitaker sight record; Ouazangou massif (20°44'56.4"S, 164°30'16.9"E): Astrongatt & le Breton (2011); Taavao, Pointe de Vavouto (21°00'39.2"S, 164°40'50.5"E): A.H. Whitaker sight record; Mè Ewâ, 6 km SE Poro (21°19'23.9"S, 165°46'07.0"E): A.H. Whitaker sight record; Kotabo, Presqu'île Bogota (21°30'17.4"S, 166°01'40.8"E): A.H. Whitaker sight record; Chetorè Kwèdè, Haut Nakéty, 8 km E Nakéty (21°33'03.1"S, 166°06'43.2"E): A.H. Whitaker sight record; PROVINCE SUD: Mine Galliéni, Mt Vulcain, Tontouta Valley (21°54'07.1"S, 166°21'06.5"E): A.H. Whitaker sight record.

*Rhacodactylus leachianus*:

PROVINCE NORD: Oubatche (20°25'35"S, 164°38'00"E): NMBA 7056–58, 7095; Pamboa Gegend (20°31'20"S, 164°32'00"E): NMBA 7053–54; Tao (20°33'40"S, 164°48'00"E): MCZ R-15967, NMBA 7059–60, 7062, 7064–65; Hienghène (20°41'30"S, 164°56'30"E): CAS 80881, NMBA 7066–67; Touho (20°47'00"S, 165°14'00"E): CAS 159510; St. Therese, 15 km NE Poindimié, Vallée d'Amoa (20°58'00"S, 165°13'20"E): CAS 156690; Ponérihouen (21°04'30"S, 165°24'00"E): NMW 19668; Vallée de Nimbaye, near Ponérihouen (21°06'00"S, 165°21'00"E): CAS 165890; Mt. Aoupinié (21°09'19"S, 165°19'12"E): AMS R146420, CAS 200266; Houaïlou (21°17'00"S, 165°37'30"E): ZFMK 55041–42, 73575; upper Houaïlou valley (21°20'30"S, 165°26'10"E): BMNH 1926.9.17.6; Île Némou (21°40'40"S, 166°23'10"E): MCZ Z-39196. PROVINCE SUD: Col d'Amieu (21°36'20"S, 165°48'00"E): USNM 267945.6140923; Sarraméa (21°38'S, 165°50'E): ZFMK 45845; La Foa (21°42'00"S, 165°58'00"E): ZFMK 25397, 36270, 46983, 55040; Mt. Mou (22°04'S, 166°21'E): CAS 172734; Mt. Gouémba (= Wô Bwa Wîwâ), 3 km S La Fausse Yaté Bridge (22°10'S, 166°57'E): AMS R90386, R118099, R123492–93; Mt. Koghis (22°10'39.09"S, 166°28'39.36"E): AMS 174500; Col d'Tonghoue (22°11'30"S, 166°28'45"E): YPM 14621; Forêt de Yahoué (22°12'10"S, 166°29'40"E): CAS 165857, 172735; Yahoué Valley, vicinity of Nouméa (22°12'30"S, 166°29'35"E): CAS 80879–80, CAS-SU7719; vicinity Goro (22°17'15"S, 167°00'40"E): CAS 203066–67, CAS 250860; Plaine des Lacs, Kwa Néie (22°18'55"S, 166°54'47"E): AMS R152651; Plaine des Lacs: SMF 65881; Île Konubutr (22°34'00"S, 167°30'45"E): CAS 250864; Gite Kodjeue, Île des Pins (22°35'55"S, 167°25'10"E): CAS 182197; Îlot Taré (22°38'30"S, 167°32'00"E): CAS 250863; Îlot Môrô (22°39'15"S, 167°23'35"E): CAS 250841–45; Îlot Bayonnaise (22°40'09"S, 167°25'24"E): CAS 203068, 214446; Nuû Ana (22°44'03"S, 167°35'00"E): CAS 250862; Nuû Ami (22°45'35"S, 167°34'02"E): CAS 250861; Île des Pins (no precise locality): BMNH 53.8.16.13, MTKD/D/35750\* (**paratype** *R. l. henkeli*), SMF 75976\* (**holotype** *R. l. henkeli*), ZFMK 55266, 73576, ZSM 854/2001. PROVINCE DES ÎLES (in error): Loyalty Islands [sic] AMNH 62686. NEW CALEDONIA (no precise locality): BMNH 85.11.16.1, 86.3.17.1, FMNH 270134, IRSNB 806, MHNG 769.94, MLI\* [lost] (**holotype** *R. aubrianus*), MMNH (1 spec., no number), MNHN 702, 1483, 4210, 6687 (**holotype**), 86.24, NHMG 657(1–2), NMW 17928, SMF SMF 59030–31, 60655 (captive born), 104066, YPM 10171, ZIN 7947, ZMB 383; ZMH R02717, R02831, ZSM 117/1920, 824/1997 (captive/embryo).

ADDITIONAL UNVOUCHERED RECORDS MAPPED: PROVINCE NORD: Mt. Mandjelia (20°24'15"S, 164°31'18"E):

A. Bauer & R. Sadlier sight record; Access track to Mt Panié (20°33'16.6"S, 164°47'21.8"E): A.H. Whitaker sight record; Kokengone River (20°51'15.5"S, 165°14'15.7"E): M. Sanchez sight record. PROVINCE SUD: Île Caanawa (22°31'55.0"S, 167°25'23.0"E): Seipp & Klemmer (1994); Kucaariüü, Île des Pins (-22°35'10.7"S, 167°31'14.5"E): A.H. Whitaker sight record; Île Kuumo (22°37'20.0"S, 167°24'30"E): Seipp & Henkel (2000); Du Ami (22°37'30.5"S; 167°16'47.5"E): Cimelli (2009); Du Ana (22°37'32.9"S, 167°18'45.7"E): Seipp & Klemmer (1994); Îlot Brosse (22°42'35.0"S, 167°27'00.0"E): Cimelli (2009).

*Rhacodactylus trachycephalus*:

PROVINCE SUD: Île des Pins (no precise locality): IRSNB 2.532 (formerly IRSNB 786, **lectotype**), 2.533 (formerly IRSNB 786 $\beta$ , **paralectotype**); Îlot Môrô (22°39'03"S, 167°23'35"E): CAS 203064, 214440.

*Rhacodactylus trachyrhynchus*:

PROVINCE NORD: Mt. Aoupinié (21°09'19"S, 165°19'12"E): AMS R146417–19, CAS 200267–68; Pindaï (21°20'02"S, 164°58'21"E): CAS 200269; Coula-Boréaré (21°21'10"S, 165°27'20"E): NMBA7039; Bourail (21°31'00"S, 165°28'30"E): ZFMK 46982; Ciu, oberh. Canala (21°33'45"S, 165°58'55"E): MCZ R-19647, NMBA 7041–42, 7044, 7046. PROVINCE SUD: La Foa (21°42'00"S, 165°50'00"E): ZFMK 25398, 29112 (captive bred), 46106; Mt. Gouémba (= Wô Bwa Wîwâ), 3km S La Fausse Yaté Bridge (22°10'S, 166°57'E): AMS R78129–32, 90185; Mt. Koghis (22°10'43"S, 166°30'20"E): collection and number unknown\* (Vences et al. 2001); bnear Nouméa: BMNH 80.6.17.5a–b, 86.3.11.2–4; vicinity Goro (22°17'15"S, 167°00'40"E): CAS 203065; NEW CALEDONIA (no precise locality): BMNH 1920.1.20.305, IRSNB 786 $\gamma$ , 786 $\delta$ , MLI\* [lost] (**holotype**), MNHN 700, 5789, 85.756, 86.271–72, 1974.803, ZFMK 31806.