

Zoologia Neocaledonica 8

Biodiversity studies in New Caledonia

edited by **Éric Guilbert**, **Tony Robillard**, **Hervé Jourdan** & **Philippe Grandcolas**

MUSÉUM
NATIONAL D'HISTOIRE NATURELLE

**PUBLICATIONS
SCIENTIFIQUES**

MÉMOIRES DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE

Directeur de la publication :

Thomas GRENON, directeur général

Rédacteur en chef (Editor-in-Chief) :

Tony ROBILLARD

Rédacteur (Editor) :

Philippe BOUCHET

Secrétaires de rédaction (Copy editors) :

Bernadette GOTTINI-CHARLES

Albéric GIRARD

Adresse (Address) :

Mémoires du Muséum national d'Histoire naturelle

CP 41 - 57, rue Cuvier

F-75005 Paris

Tél. : [33] 01 40 79 34 37

Fax. : [33] 01 40 79 38 08

e-mail : memoires@mnhn.fr

Les *Mémoires du Muséum national d'Histoire naturelle* publient des travaux originaux majeurs, tels que des monographies ou des volumes à auteurs multiples. Les auteurs sont invités, pour toutes les questions éditoriales, à prendre contact avec le rédacteur en chef. Les manuscrits peuvent être en français ou en anglais.

Parution et prix irréguliers. Les ordres permanents d'achat et les commandes de volumes séparés sont reçus par le **Service des Publications Scientifiques, Diffusion (France)**. Une liste des derniers titres parus figure en page 3 de couverture.

Imprimé sur papier non acide

The *Mémoires du Muséum national d'Histoire naturelle* publish major original contributions, such as monographs or multi-authored volumes. Prospective authors should contact the Editor-in-Chief. Manuscripts in French or in English will be considered.

Volumes are published at irregular intervals, and with different irregular prices. Standing orders and orders for single volumes should be directed to the **Service des Publications Scientifiques du Muséum (France)**. Recently published memoirs are listed on page 3 of the cover.

Printed on acid-free paper

Vente / Sales :

Muséum national d'Histoire naturelle

Publications Scientifiques

Diffusion : Ahmed ABDYOU

CP 41 - 57, rue Cuvier

F-75005 Paris

Tél. : [33] 01 40 79 48 05

Fax : [33] 01 40 79 38 40

e-mail : diff.pub@mnhn.fr

<http://www.mnhn.fr/publication/>

Cover photograph

View on the bay of Ouaième (New Caledonia, Province Nord), 2 novembre 2010

Vue sur la baie de la Ouaième (Nouvelle-Calédonie, Province Nord), 2 novembre 2010

Photo by Frédéric Legendre, MNHN.

Published volume

Volume 1 : *Mémoires du Muséum national d'Histoire naturelle* 142 (A) : 1-158 (1988). ISBN : 2-85653-163-6.

Volume 2 : *Mémoires du Muséum national d'Histoire naturelle* 149 (A) : 1-358 (1990). ISBN : 2-85653-179-2.

Volume 3 : *Mémoires du Muséum national d'Histoire naturelle* 157 : 1-218 (1993). ISBN : 2-85653-205-5.

Volume 4 : *Mémoires du Muséum national d'Histoire naturelle* 171 : 1-399 (1997). ISBN : 2-85653-505-4.

Volume 5 : *Mémoires du Muséum national d'Histoire naturelle* 187 : 1-282 (2002). ISBN : 2-85653-536-4.

Volume 6 : *Mémoires du Muséum national d'Histoire naturelle* 197 : 1-326 (2008). ISBN : 978-2-85653-605-6.

Volume 7 : *Mémoires du Muséum national d'Histoire naturelle* 198 : 1-440 (2009). ISBN : 978-2-85653-618-6.

Volume 8 : *Mémoires du Muséum national d'Histoire naturelle* 206 : 1-315 (2014). ISBN : 978-2-85653-707-7.

Zoologia Neocaledonica 8

Biodiversity studies in New Caledonia

ISBN : 978-2-85653-707-7

ISSN : 1243-4442

© Publications Scientifiques du Muséum, Paris, 2014

Photocopies

Les Publications Scientifiques du Muséum adhèrent au Centre Français d'Exploitation du Droit de Copie (CFC), 20, rue des Grands Augustins, 75006 Paris. Le CFC est membre de l'International Federation of Reproduction Rights Organisations (IFRRO). Aux États-Unis d'Amérique, contacter le Copyright Clearance Center, 27, Congress Street, Salem, Massachusetts 01970.

www.cfcopies.com

www.ifrro.org

www.copyright.com

Photocopies

The Scientific Publications of the Muséum adhere to the Centre Français d'Exploitation du Droit de Copie (CFC), 20, rue des Grands Augustins, 75006 Paris. The CFC is a member of International Federation of Reproduction Rights Organisations (IFRRO). In USA, contact the Copyright Clearance Center, 27, Congress Street, Salem, Massachusetts 01970.

www.cfcopies.com

www.ifrro.org

www.copyright.com

Zoologia Neocaledonica 8

Biodiversity studies in New Caledonia

Mémoires du Muséum national d'Histoire naturelle

Tome 206

Éric GUILBERT¹, Tony ROBILLARD¹, Hervé JOURDAN² & Philippe GRANDCOLAS¹

¹ Muséum national d'Histoire naturelle
Institut de Systématique
Évolution, Biodiversité
ISYEB - UMR 7205 CNRS, UPMC, EPHE
CP 50, 45, rue Buffon
75005 Paris, France

² Institut Méditerranéen de Biodiversité et
d'Écologie marine et continentale (IMBE)
Aix-Marseille Université - CNRS - IRD - UAPV
Centre IRD Noumea
BP A5, 98848 Noumea
New Caledonia

Publications Scientifiques du Muséum

Paris

2014

CONTENTS

INTRODUCTION	9
Éric GUILBERT, Tony ROBILLARD, Hervé JOURDAN & Philippe GRANDCOLAS	
New data on <i>Dierogekko</i> (Squamata: Gekkota: Diplodactylidae), with the description of a new species from Île Baaba , Province Nord, New Caledonia	13
Phillip SKIPWITH, Todd JACKMAN, Anthony H. WHITAKER, Aaron M. BAUER & Ross A. SADLER	
The New Caledonian Leopard Skink <i>Lacertoides pardalis</i> (Reptilia: Scincidae); a review of the species' morphology, distribution, behavior and conservation	31
Ross A. SADLER, Glenn M. SHEA, Hervé JOURDAN, Anthony H. WHITAKER & Aaron M. BAUER	
Cryptic speciation in the New Caledonian lizard genus <i>Nannoscincus</i> (Reptilia: Scincidae) including the description of a new species and recognition of <i>Nannoscincus fuscus</i> Günther	45
Ross A. SADLER, Aaron M. BAUER, Perry L. WOOD Jr., Sarah A. SMITH, Anthony H. WHITAKER & Todd JACKMAN	
Bocourt's terrific Skink, <i>Phoboscincus bocourti</i> (Brocchi, 1876), and the Monophyly of the Genus <i>Phoboscincus</i> Greer, 1974 (Reptilia: Scincidae)	69
Ivan INEICH, Ross A. SADLER, Aaron M. BAUER, Todd R. JACKMAN & Sarah A. SMITH	
Localized endemism in the southern ultramafic bio-region of New Caledonia as evidenced by the lizards in the genus <i>Sigaloseps</i> (Reptilia: Scincidae), with descriptions of four new species	79
Ross A. SADLER, Aaron M. BAUER, Perry L. WOOD Jr., Sarah A. SMITH, Anthony H. WHITAKER, Hervé JOURDAN & Todd JACKMAN	
High elevation endemism on New Caledonia's ultramafic peaks – a new genus and two new species of scincid lizard	115
Ross A. SADLER, Aaron M. BAUER, Sarah A. SMITH, Glenn M. SHEA & Anthony H. WHITAKER	
New data on freshwater fish of New Caledonia	127
Philippe KEITH, Clara LORD, Laura TAILLEBOIS & Pierre FEUTRY	
The New Caledonian and Fijian species of Aterpini and Gonipterini (Coleoptera: Curculionidae)	133
Guillermo KUSCHEL	
The blind weevils of Myrtonymina in New Caledonia and Australia (Curculionidae: Curculioninae: Erirhinini: Myrtonymina)	165
Guillermo KUSCHEL	

<i>Exocelina nehoue</i> n. sp. from New Caledonia, with a new synonym and new collecting records for other species in the genus (Coleoptera: Dytiscidae)	181
Michael BALKE, Jiří HÁJEK, Lars HENDRICH & Günther WEWALKA	
A new species, new records, and notes on biology of New Caledonian <i>Scirtes</i> Illiger (Insecta: Coleoptera: Scirtidae)	191
Rafał RUTA	
<i>Corindia</i> (Diptera: Dolichopodidae) from New Caledonia and the Papuan Region	201
Daniel J. BICKEL	
<i>Pindaia</i> (Diptera: Dolichopodidae) a new genus from New Caledonia and Australia	209
Daniel J. BICKEL	
The water bugs (Hemiptera-Heteroptera: Gerromorpha & Nepomorpha) of New Caledonia: Diversity, ecology and biogeographical significance	219
Jakob DAMGAARD & Herbert ZETTEL	
New Caledonia as an evolutionary cradle: a re-appraisal of the jaw-moth genus <i>Sabatinca</i> (Lepidoptera: Micropterigidae) and its significance for assessing the antiquity of the island's fauna	239
George W. GIBBS & David C. LEES	
Owlfly of New Caledonia. <i>Suhpalacsa caledon</i> McLachlan, 1871 (Neuroptera: Ascalaphidae)	267
Roland DOBOSZ & Ábrahám LEVENTE	
Redefinition of the cricket genus <i>Protathra</i> Desutter-Grandcolas, 1997 (Orthoptera, Grylloidea, Phalangopsidae), with description of the calling song of <i>Protathra centralis</i> Desutter-Grandcolas, n. sp.	277
Laure DESUTTER-GRANDCOLAS, Tony ROBILLARD & Jérémy ANSO	
Three new species and a synonymy of the genus <i>Nobarnus</i> (Insecta: Heteroptera: Tingidae)	289
Éric GUILBERT	
Diversity and distribution of the genus <i>Rothsilpha</i> (Dictyoptera, Blattidae) in New Caledonia: Evidence from new microendemic species	299
Philippe GRANDCOLAS, Romain NATTIER, Roseli PELLENS & Frédéric LEGENDRE	
INDEX TAXONOMIQUE	309

INTRODUCTION

New Caledonia has been characterized as one of the major hot spots of biodiversity because of high levels of specific richness, endemism and threats in spite of the small size (less than 19,000 km²) of the archipelago (Myers *et al.* 2000; Kier *et al.* 2009). This peculiar combination of characteristics makes necessary both scientific study and conservation planning in the context of the current biodiversity crisis (Beauvais *et al.* 2006). Since several decades, the series Zoologia Neocaledonica significantly contributes to the scientific study of biodiversity and the last three volumes published still revealed a large number of new species in many different animal groups, from vertebrates to insects and other arthropods (Najt & Grandcolas 2002; Grandcolas 2008, 2009). This accumulation of studies highlights the characteristics of New Caledonian biodiversity: the main island harbors many microendemic species, the discovery of which is difficult because of the complex mountainous landscape and the necessary field work carried out by many specialists coming from all over the world (Pellens & Grandcolas 2010). In the emergency situation of a hotspot, both the scientific studies and the conservation planning need to be conducted with acceleration by all means. In this context, some attempts of rapid assessment have been carried out which show promising results (Gasc *et al.* 2013). Also, recently developed tools such as niche modeling have been used with the hope to better understand the distribution of New Caledonian species even when the spatial sampling is still sparse (Murienne *et al.* 2009; Kumar & Stohlgren 2009; Nattier *et al.* 2013). All these efforts need to be made simultaneously, given that rapid assessments and ecological modeling calibrate with and feed on extant data. There is no such tool, even the most fashioned molecular ones like barcoding or environmental genomics that do not finally refer to taxonomic data.

Therefore, we value and thank very much the studies published in the present volume that patiently contribute to the knowledge of local biodiversity. Most of these taxonomic works and inventories were connected in some ways to evolutionary and ecological studies that have been or will be published elsewhere. In that way, taxonomy is both an engine for biodiversity research, revealing species characteristics and patterns that could be studied further, and a result of question-driven studies the vouchers of which are named, saved and let available for everybody.

The new species described in this volume will undoubtedly help contributing both conservation planning and scientific research. There are many interesting questions which depend on such improved species sampling, from the origin of New Caledonian clades to the dynamics of speciation and microendemism, and including ecosystem functioning. Evolutionary questions need to be placed in a refined time scale by molecular dating which can be only obtained with an accurate taxon sampling. Recent case studies allowed reviews to be published and to converge on the same perspective (Grandcolas *et al.* 2008; Cruaud *et al.* 2012; Pillon 2012). Molecular dates and especially their standard deviation are consistent with colonization posterior to the latest emersion episode of the island (ca 37 ± 3 My, Cluzel *et al.* 2012). Local endemism has also been shown for the first time to follow an interesting trend with distribution areas increasing with time in a group of insects, suggesting that extreme microendemism may be related to recent events of speciation (Nattier *et al.* 2012) and this result is calling for parallel studies in other groups. As to conservation planning (Pellens & Grandcolas 2010), it should be critically discussed according to the most recent taxonomic studies as well (*e.g.*, Barrabé *et al.* 2014; Brescia *et al.* 2008; Jaffré *et al.* 2010; Ungricht *et al.* 2005). This volume of Zoologia Neocaledonica will contribute to fuel further biodiversity studies and conservation strategies.

INTRODUCTION

La Nouvelle-Calédonie est considérée comme l'un des principaux points sensibles de biodiversité en raison de niveaux élevés de richesse spécifique, d'endémisme et de risques d'extinction, et ce malgré la petite taille (moins de 19 000 km²) de l'archipel (Myers *et al.* 2000 ; Kier *et al.* 2009). Cette combinaison particulière de caractéristiques rend indispensable à la fois son étude scientifique et une planification de la conservation, dans le contexte de la crise actuelle de la biodiversité (Beauvais *et al.* 2006). Depuis plusieurs décennies, la série *Zoologia Neocaledonica* contribue de manière significative à l'étude scientifique de la biodiversité et les trois derniers volumes publiés ont révélé encore un grand nombre d'espèces nouvelles dans de nombreux groupes d'animaux différents, des vertébrés aux insectes et autres arthropodes (Najt & Grandcolas 2002 ; Grandcolas 2008, 2009). L'ensemble de ces études permet de mettre en évidence les caractéristiques de la biodiversité néocalédonienne : la Grande Terre abrite de nombreuses espèces microendémiques dont la découverte reste difficile en raison du paysage montagneux complexe et du travail de terrain effectué par de nombreux spécialistes du monde entier (Pellens & Grandcolas 2010). Dans la situation d'urgence qui est celle d'un point sensible, tous les moyens doivent être employés pour accélérer la production des études scientifiques et la planification de la conservation. Dans ce contexte, quelques tentatives d'évaluation rapide de la biodiversité ont montré des résultats prometteurs (Gasc *et al.* 2013). Des outils récemment développés comme la modélisation des niches ont également été utilisés dans l'espoir de mieux comprendre la répartition des espèces de Nouvelle-Calédonie même si leur échantillonnage est encore trop clairsemé au plan spatial (Murienné *et al.* 2009 ; Kumar & Stohlgren 2009 ; Nattier *et al.* 2013). Tous ces efforts doivent être faits de manière simultanée, étant donné que les résultats des évaluations rapides et des modélisations écologiques ne peuvent être calibrés qu'avec les données taxonomiques existantes. En effet, tous les outils, même les plus puissants et les plus à la mode, comme les codes-barres moléculaires ou la génomique environnementale n'ont de valeur qu'en référence aux données taxonomiques.

Par conséquent, les études publiées dans le présent volume et qui contribuent patiemment à la connaissance de la biodiversité locale sont extrêmement bienvenues. La plupart de ces travaux et inventaires taxonomiques sont par ailleurs liés à des études évolutives ou écologiques en cours. De ce point de vue, la taxonomie est à la fois un moteur pour la recherche sur la biodiversité, révélant espèces caractéristiques et modèles qui pourraient être étudiés plus avant, et une résultante des études scientifiques dont les spécimens de référence sont nommés, enregistrés et tenus à disposition de tous.

Les nouvelles espèces décrites dans ce volume permettront sans aucun doute de contribuer à la fois à la connaissance de la biodiversité et à la planification de la conservation. Il y a beaucoup de questions intéressantes qui dépendent de cet échantillonnage, depuis l'origine de clades de Nouvelle-Calédonie jusqu'à la dynamique de la spéciation et du microendémisme, en passant par le fonctionnement des écosystèmes. Toutes les questions d'évolution demandent une chronologie précise obtenue par datation moléculaire, elle-même liée à un échantillonnage taxonomique précis. De fait, de nombreuses études systématiques récentes ont permis la publication de plusieurs revues de synthèse qui convergent toutes vers le même point de vue (Grandcolas *et al.* 2008 ; Cruaud *et al.* 2012 ; Pillon 2012). Les datations moléculaires et en particulier leur écarts-types sont ainsi compatibles avec un scénario de colonisation postérieure au dernier épisode d'émersion de l'île (environ 37 ± 3 Ma, Cluzel *et al.* 2012). Pour la première fois, il a été également montré que les aires de répartition des espèces microendémiques augmentent avec leur âge, ce qui signifierait que des événements très récents de spéciation sont à l'origine du microendémisme le plus extrême (Nattier *et al.* 2012). Ce résultat obtenu chez un groupe d'Insectes gagnerait d'ailleurs à être généralisé avec des études menées sur d'autres groupes d'organismes. Quant à la planification de la conservation (Pellens & Grandcolas 2010), elle doit être établie de manière critique en référence aux études taxonomiques les plus récentes (par exemple, Barrabé *et al.* 2014 ; Brescia *et al.* 2008 ; Jaffré *et al.* 2010 ; Ungricht *et al.* 2005). Ce volume des *Zoologia Neocaledonica* contribuera certainement à ces deux objectifs.

REFERENCES

- BARRABE L., MAGGIA L., PILLON Y., RIGAULT F., MOULY A., DAVIS A.P. & BUEKRI S. 2014 — New Caledonian lineages of *Psychotria* (Rubiaceae) reveal different evolutionary histories and the largest documented plant radiation for the archipelago. *Molecular Phylogenetics and Evolution* 71: 15-35.
- BEAUVAIS M.L., COLENO A. & JOURDAN H. (eds) 2006 — *Les espèces envahissantes dans l'archipel néo-calédonien. Invasive species in the New Caledonian Archipelago*. IRD Éditions, Paris, 259 p.
- BRESCIA F.M., PÖLLABAUER C.M., POTTER R.A. & ROBERTSON A.W. 2008 — A review of the ecology and conservation of *Placostylus* (Mollusca: Gastropoda: Bulimulidae) in New Caledonia. *Molluscan Research* 28(2): 111-122.
- CLUZEL D., MAURIZOT P., COLLOT J. & SEVIN B. 2012 — An outline of the geology of New Caledonia; from Permian-Mesozoic South-Gondwana active margin to Tertiary obduction and supergene evolution. *Episodes* 35: 72-86.
- CRUAUD A., JABBOUR-ZAHAB R., GENSON G.E., UNGRICHT S. & RASPLUS J.Y. 2012 — Testing the emergence of New Caledonia: Fig wasp mutualism as a case study and a review of evidence. *Plos ONE* 7(2): e30941.
- GASC A., SUEUR J., PAVOINE S., PELLENS R. & GRANDCOLAS P. 2013 — Biodiversity sampling using a global acoustic approach: Contrasting sites with microendemism in New Caledonia. *PLoS ONE* 8(5): e65311.
- GRANDCOLAS P. (ed.) 2008 — Zoologia Neocaledonica 6. Biodiversity studies in New Caledonia. *Mémoires du Muséum national d'Histoire naturelle*, Paris 197: 1-326.
- GRANDCOLAS P. (ed.) 2009 — Zoologia Neocaledonica 7. Biodiversity studies in New Caledonia. *Mémoires du Muséum national d'Histoire naturelle*, Paris 198: 1-440.
- GRANDCOLAS P., MURIENNE J., ROBILLARD T., DESUTTER-GRANDCOLAS L., JOURDAN H., GUILBERT E. & DEHARVENG L. 2008 — New Caledonia: a very old Darwinian island? *Philosophical Transactions of the Royal Society of London*, B 363: 3309-3317.
- JAFFRE T., MUNZINGER J. & LOWRY P.P. 2010 — Threats to the conifer species found on New Caledonia's ultramafic massifs and proposals for urgently needed measures to improve their protection. *Biodiversity and Conservation* 19: 1485-1502.
- KIER G., KREFT H., LEE T.M., JETZ W., IBISCH P.L., NOWICKIC C., MUTKE J. & BARTHLOTT W. 2009 — A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences of the USA* 106 (23): 9322-9327.
- KUMAR S. & STOHILGREN T.J. 2009 — Maxent modeling for predicting suitable habitat for threatened and endangered tree *Canacomyrica monticola* in New Caledonia. *Journal of Ecology and Natural Environment* 1: 94-98.
- MURIENNE J., GUILBERT E. & GRANDCOLAS P. 2009 — Species diversity in the New Caledonian endemic genera *Cephalidiosus* and *Nobarnus* (Insecta: Heteroptera: Tingidae), an approach using phylogeny and species distribution modeling. *Biological Journal of the Linnean Society* 97: 177-184.
- MYERS N., MITTERMEIER R.A., MITTERMEIER C.G., DA FONSECA G.A.B. & KENT J. 2000 — Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- NAJT, J. & GRANDCOLAS, P. (eds) 2002 — Zoologia Neocaledonica 5. Systématique et endémisme en Nouvelle-Calédonie. *Mémoires du Muséum national d'Histoire naturelle* 187: 1-283.
- NATTIER R., GRANDCOLAS P., ELIAS M., DESUTTER-GRANDCOLAS L., JOURDAN H., COULOUX A. & ROBILLARD T. 2012 — Secondary sympatry caused by range expansion informs on the dynamics of microendemism in a biodiversity hotspot. *Plos ONE* 7(11): e48047.
- NATTIER R., GRANDCOLAS P., PELLENS R., JOURDAN H., COULOUX A., POULAIN S. & ROBILLARD T. 2013 — Climate and soil together explain the distribution of microendemic species in a biodiversity hotspot. *PLoS ONE* 8(12): e80811.
- PELLENS R. & GRANDCOLAS P. 2010 — Conservation and management of the biodiversity in a hotspot characterized by short range endemism and rarity: the challenge of New Caledonia, in RESCIGNOV. & MALETTA S. (eds), *Biodiversity Hotspots*, Nova Publishers, Hauppauge, New York: 139-151.
- PILLON Y. 2012 — Time and tempo of diversification in the flora of New Caledonia. *Botanical Journal of the Linnean Society* 170(3): 288-298.
- UNGRICT S., RASPLUS J.Y. & KJELLBERG F. 2005 — Extinction threat evaluation of endemic fig trees of New Caledonia: Priority assessment for taxonomy and conservation with herbarium collections. *Biodiversity and Conservation* 14(1): 205-232.

New data on *Dierogekko* (Squamata: Gekkota: Diplodactylidae), with the description of a new species from Île Baaba, Province Nord, New Caledonia

Phillip Skipwith ^(1,4), Todd Jackman ⁽¹⁾, †Anthony H. Whitaker ⁽²⁾, Aaron M. Bauer ⁽¹⁾ & Ross A. Sadlier ⁽³⁾

⁽¹⁾ Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085-1699, USA
aaron.bauer@villanova.edu

⁽²⁾ Whitaker Consultants Limited, 270 Thorpe-Orinoco Road, Orinoco, R.D. 1, Motueka 7196, New Zealand (deceased)

⁽³⁾ Department of Herpetology, Australian Museum, 6 College Street, Sydney 2000, New South Wales, Australia

⁽⁴⁾ Museum of Vertebrate Zoology, University of California, Berkeley, California 94720, USA

ABSTRACT

The diplodactylid gecko genus *Dierogekko* is endemic to the northern Grande Terre of New Caledonia and the adjacent ultramafic offshore islands. All species are allopatric except *D. poumensis* and *D. inexpectatus*, both of which occur on Sommet Poum. The validity of the latter species, described on the basis of a single female, is confirmed by a recently collected series of specimens from Paévala. *Dierogekko inexpectatus* appears limited to the northern portion of Sommet Poum, where it is restricted to closed forest remnants. Based on its tiny area of occurrence and existing threats from mining, wildfires, invasive weeds, and a diversity of invasive animals, it is assessed as Critically Endangered. A molecular phylogenetic analysis of *Dierogekko* confirms previously proposed relationships and reveals a new species level taxon from Île Baaba, off the northern tip of the Grande Terre. The specimen is known from a single female, but is distinguished from its congeners by its small size (<38 mm SVL) and narrow, divided subdigital scansors. It is separated from all other *Dierogekko* by an uncorrected ND2 divergence of 6-15% (Tajima-Nei distance 6-17%). It is vulnerable to wildfires, habitat degradation and introduced mammalian predators and fire ants and is considered to be Critically Endangered.

RÉSUMÉ

Nouvelles données sur *Dierogekko* (Squamate : Gekkota : Diplodactylidae), avec la description d'une nouvelle espèce de l'île Baaba, Province Nord, Nouvelle Calédonie.

Le genre de gecko diplodactylide *Dierogekko* est endémique du nord de la Grande Terre de Nouvelle-Calédonie et les îles adjacentes ultramafiques. Toutes les espèces sont allopatriques sauf *D. poumensis* et *D. inexpectatus*, qui tous deux se trouvent sur le sommet de Poum. La validité de cette dernière espèce, décrite sur la base d'une seule femelle, est confirmée par une série de spécimens récemment collectés à Paévala. *Dierogekko inexpectatus* semble limitée à la partie nord du Sommet de Poum, où elle est limitée aux restes de forêts denses. Sur la base de sa minuscule zone d'occurrence et les menaces actuelles de l'exploitation minière, les incendies de forêt, les mauvaises herbes envahissantes, et une diversité d'animaux exotiques, cette espèce est considérée en risque critique d'extinction. Une analyse phylogénétique moléculaire de *Dierogekko* confirme les relations proposées précédemment et dévoile un nouveau taxon de rang spécifique des espèces de l'Île Baaba, au large de la pointe nord de la Grande Terre. Le spécimen est connu à partir d'une seule femelle, mais se distingue de ses congénères par sa petite taille (<38 mm SVL) et ses lamelles subdigitales étroites et divisées. Il est séparé de tous les autres *Dierogekko* par une divergence ND2 non corrigée de 6-15% (Tajima-Nei distance 6-17%). Il est vulnérable aux incendies de forêt, à la dégradation de l'habitat et aux mammifères prédateurs introduits ainsi qu'aux fourmis électriques et il est considéré en danger critique.

INTRODUCTION

The genus *Dierogekko* was established (Bauer *et al.* 2006) to accommodate a clade of small, nimble New Caledonian diplodactylid geckos that had previously been allocated to the genus *Bavayia* Roux, 1913. It included the species originally described as *Bavayia validiclavis* Sadlier, 1989 from Mt. Panié and Mt. Mandjélia in the Panié Massif, as well as seven new



FIGURE 1

Comparison of the two species of *Dierogekko* occurring on Sommet Poum: Left, *D. inexpectatus*; Right, *D. poumensis*. Note the darker mid-dorsal stripe and bright white dorsolateral stripes over the tail base in the latter species.

species, each endemic to single areas on or near ultramafic peaks in the northwest of the Grande Terre (Whitaker *et al.* 2004; Bauer *et al.* 2006). At the time of the description of the new taxa and erection of the genus, phylogenetic evidence from the mitochondrial ND2 gene and the RAG-1 nuclear gene were presented to support the recognition of each taxon as a distinct lineage. Only in one case were two species found to occur on the same ultramafic massif; *D. poumensis* and *D. inexpectatus* (Figure 1) occur in strict sympatry on Sommet Poum (414 m a.s.l.) (Figure 2). At the time of description the latter species was known from only a single individual. This was a female lacking precloacal pores, an important diagnostic feature for species within this group and many other diplodactylid geckos.

Subsequent surveys of the *D. inexpectatus* type locality, Paevala, and other areas of the Poum massif in 2003 and 2005 failed to locate additional material (Bauer *et al.* 2006). In 2006 the Poum massif was the target of an intensive lizard survey with particular emphasis on *Dierogekko* and *Oedodera* (Whitaker & Whitaker 2007a). No specimens of *Dierogekko inexpectatus* were found at the type locality, which was found to have become heavily infested with introduced fire ants (*Wasmannia auropunctata*), but a new population was found in a closed forest remnant ~270 m to the north. A more detailed survey in 2007, specifically targeting *Dierogekko inexpectatus*, failed to detect the species at any additional sites (Whitaker & Whitaker 2008).

Specimens and associated field data collected during the 2006 and 2007 surveys have provided crucial new data on the morphology, ecology and behaviour of *D. inexpectatus* and we take this opportunity to reevaluate its diagnostic features and report on variation and biology of this endangered taxon. Further, we reevaluate phylogenetic relationships within *Dierogekko* based on the mitochondrial marker ND2 and the relatively rapidly evolving nuclear gene, KIF24. A single individual from Île Baaba is identified as genetically distinct from all known species and is described as the ninth species in the genus.



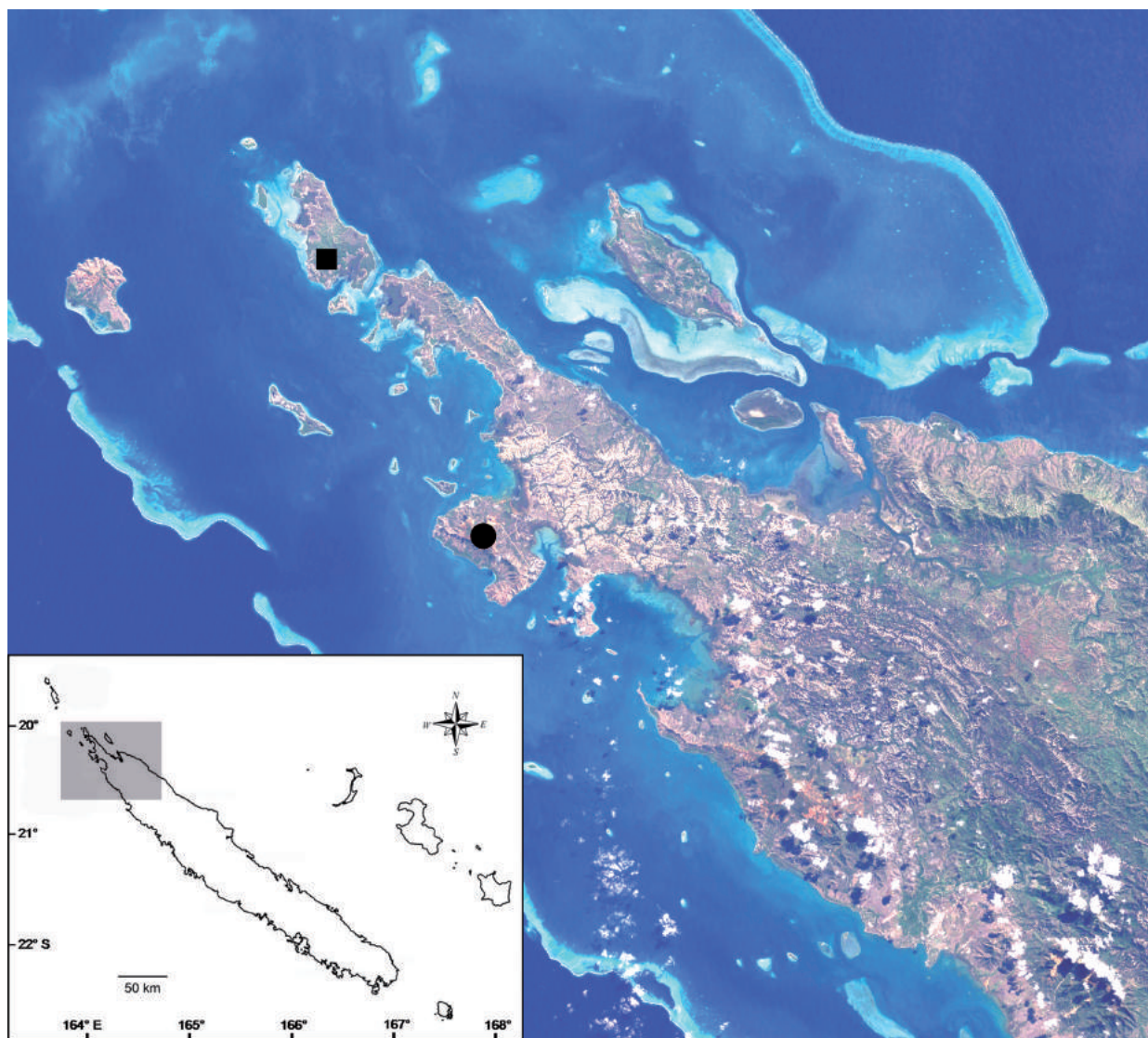


FIGURE 2

Map of northern New Caledonia illustrating the position of Sommet Poum (*Dierogecko inexpectatus* - circle) and Île Baaba (*D. baaba* - square). Image from the Millenium Coral Reef Landsat Archive.

MATERIAL AND METHODS

MORPHOLOGY

The following measurements (to the nearest 0.1 mm) were taken with DigiCal digital calipers: 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), crus length (CrusL; from base of heel to knee); tail length (TailL; from vent to tip of tail), tail width (TailW; measured at widest point of tail); head length (HeadL; distance between retroarticular process of jaw and snout-tip), head width (HeadW; maximum width of head), head height (HeadH; maximum height of head, from occiput to underside of jaws), ear length (EarL; longest dimension of ear); forearm length (ForeaL; from base of palm to elbow); orbital diameter (OrbD; greatest diameter of orbit), nares to eye distance (NarEye; distance between anteriormost point of eye and 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). Measurements and scale counts based on right side of animals unless otherwise noted.

Scale counts and external observations of morphology were made using a Nikon SMZ1000 stereo dissecting microscope. Photographs of preserved specimens were taken with a Canon G11 Powershot digital camera. Comparisons were made with museum material in the collections of the California Academy of Sciences (CAS), the Australian Museum (AMS), and the Muséum national d'Histoire naturelle, Paris (MNHN). See Bauer *et al.* (2006) for a complete list.

MOLECULAR PHYLOGENETICS

Sequences were acquired from 48 individuals representing all described species of *Dierogecko*, an increase of 23 from the previous analysis (Bauer *et al.* 2006). Representatives of each of the other New Caledonian dipodactylid genera were included as outgroups (Table 1). Sequences were analyzed for 1464 bp of the mitochondrial gene ND2 and five flanking tRNAs (NADH dehydrogenase subunit 2: 1049 bp protein coding, 415 bp tRNA) and 551 bp of the nuclear gene KIF24 (kinesin family member 24). Genomic DNA was obtained using the Qiagen DNAeasy Kit from whole tissues consisting of liver, tail tips, or skeletal muscle stored in 95% EtOH. The subsequent amplification of target loci was carried out in 25 µl PCR reactions on a Eppendorf Mastercycler gradient thermocycler. Primers were initially derived from the genomes of *Gallus* and *Anolis* before gecko specific primers were designed. PCR products were visualized on 1.5% agarose gels before being purified with AMPure magnetic bead solution kit (Agencourt Bioscience, Beverly, MA, USA). These were then sequenced using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) and subjected to a final purification through the CleanSeq magnetic bead kit (Agencourt Bioscience, Beverly, MA, USA) protocol. Products were sequenced on a ABI 3730xl DNA analyzer before sequence quality was assessed using the program Geneious v4.7 (Drummond *et al.* 2006). Complete sequences were aligned by eye and manually corrected in MacClade (Maddison & Maddison 2008) after being translated into amino acid sequences.

Phylogenetic analysis included maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). MP analysis was run in PAUP v4.0 (Swofford 2002) under a full heuristic search using tree bisection-reconnection (TBR). Nodal support was designated with 1,000 nonparametric bootstrap replicates. ML was run in the program RAxML v7.2.6 (Stamatakis *et al.* 2005, 2010, Stamatakis 2006) for 1,000 rapid nonparametric bootstrap replicates. MrBayes v3.1 (Huelsenbeck & Ronquist 2003) was used for BI analysis and run for 20,000,000 generations sampling every 1,000 generations. The first 5,000 trees from each of the two independent runs were discarded as burn-in and stationarity was assessed graphically with the online program AWTY (Are we there yet?) (Nylander *et al.* 2008). Bayesian runs that reached convergence were combined in PAUP to construct a 50% majority rule consensus tree. KIF24 and the protein coding region of ND2 were partitioned based on codon position while the five tRNAs immediately following ND2 were designated to a separate partition in all ML and BI runs. These segments were individually assigned nucleotide models of evolution in Modeltest v3.7 (Posada & Crandall 1998) using Akaike Information Criterion (AIC) (Table 2).

TABLE 1

Specimens used in the molecular study and their corresponding GenBank accession numbers.

TAXON	CATALOGUE NUMBER	LOCALITY	GENBANK ACCESSION NOS.	
OUTGROUP			ND2	KIF24
<i>Bavayia aff. robusta</i>	AMS R138591	Île des Pins (22°38'S, 167°25'E)	JF972431	JF972395
<i>Bavayia geitaina</i>	AMS R148084	Mt. Koghis (22°10'18"S, 166°30'58"E)	–	JF972396
<i>Bavayia geitaina</i>	CAS 202733	Mt. Koghis (22°10'18"S, 166°30'58"E)	JF972423	–
<i>Paniegekko madjo</i>	AMS R149329	Mt. Panié (20°34'04"S, 164°46'25"E)	JF972430	JF972397
<i>Eurydactyloides symmetricus</i>	CAS 232006	Pic Ningua (21°44'36"S, 166°09'02"E)	JF972428	JF972393
<i>Oedodera marmorata</i>	AMS R161249	Paagoumène (20°29'21"S, 164°11'49"E)	JF972427	JF972392
<i>Rhacodactylus auriculatus</i>	AMS R161252	Dôme de Tiébaghi (20°27'38"S, 164°11'11"E)	JF972429	JF972394
INGROUP				
<i>Dierogekko inexpectatus</i>	CAS 248152	Sommet Poum (20°14'54.6"S, 164°01'21.9"E)	JF972442	–
<i>Dierogekko inexpectatus</i>	CAS 248153	Sommet Poum (20°14'54.6"S, 164°01'21.9"E)	–	JF972405
<i>Dierogekko inexpectatus</i>	CAS 248154	Sommet Poum (20°14'54.6"S, 164°01'21.9"E)	JF972440	JF972406
<i>Dierogekko inexpectatus</i>	AMS R175527	Sommet Poum (20°14'54.6"S, 164°01'21.9"E)	JF972439	JF972407
<i>Dierogekko inexpectatus</i>	AMS R175529	Sommet Poum (20°14'54.6"S, 164°01'21.9"E)	–	JF972408
<i>Dierogekko inexpectatus</i>	AMS R175531	Sommet Poum (20°14'54.6"S, 164°01'21.9"E)	–	JF972404
<i>Dierogekko inexpectatus</i>	AMS R161222	Sommet Poum (20°15'44"S, 164°02'07"E)	JF972441	JF972403
<i>Dierogekko insularis</i>	AMS R166974	Mariri, Île Yandé (20°02'39.4"S, 163°47'43.4"E)	JF972435	–
<i>Dierogekko insularis</i>	CAS 231857	Mariri, Île Yandé (20°02'39.4"S, 163°47'43.4"E)	JF972436	JF972411
<i>Dierogekko insularis</i>	AMS R166972	Mariri, Île Yandé (20°02'39.4"S, 163°47'43.4"E)	JF972434	–
<i>Dierogekko insularis</i>	CAS 231858	Mariri, Île Yandé (20°02'39.4"S, 163°47'43.4"E)	JF972433	–
<i>Dierogekko insularis</i>	AMS R161066	Pânan, Île Pott (19°35'06"S, 163°35'07"E)	JF972459	JF972410
<i>Dierogekko insularis</i>	AMS R161067	Pânan, Île Pott (19°35'06"S, 163°35'07"E)	KF366667	KF366658
<i>Dierogekko insularis</i>	AMS R161069	Île Art (19°42'53"S, 163°39'38"E)	JF972458	–
<i>Dierogekko insularis</i>	AMS R161070	Île Art (19°42'53"S, 163°39'38"E)	KF366666	–
<i>Dierogekko kaalaensis</i>	AMS R161095	Mt. Kaala (20°37'03"S, 164°22'49"E)	JF972455	JF972412
<i>Dierogekko kaalaensis</i>	AMS R161096	Mt. Kaala (20°37'03"S, 164°22'49"E)	JF972456	JF972413
<i>Dierogekko kaalaensis</i>	AMS R161101	Piton de Pandop (164°22'05"E, 20°35'16"S, 164°22'49"E)	JF972454	JF972414
<i>Dierogekko koniambo</i>	AMS R161114	Mt. Koniombo (20°59'51"S, 164°48'47"E)	–	JF972421
<i>Dierogekko koniambo</i>	AMS R161128	Mt. Koniombo (20°59'42"S, 164°48'56"E)	–	JF972423
<i>Dierogekko koniambo</i>	AMS R161129	Mt. Koniombo (20°59'51"S, 164°48'47"E)	JF972451	JF972422
<i>Dierogekko koniambo</i>	AMS R168036	Taavao, Pointe de Vavouto (21°00'49"S, 164°40'39"E)	JF972452	KF366659
<i>Dierogekko koniambo</i>	AMS R168037	Taavao, Pointe de Vavouto (21°00'49"S, 164°40'39"E)	JF972453	KF366660
<i>Dierogekko nehoueensis</i>	AMS R166970	Rivière Néhoulé (20°25'12.3"S, 164°13'04.5"E)	KF366663	JF972426
<i>Dierogekko nehoueensis</i>	CAS 231835	Rivière Néhoulé (20°25'03"S, 164°13'15"E)	JF972438	KF366661
<i>Dierogekko nehoueensis</i>	CAS 231855	Rivière Néhoulé (20°24'27.0"S, 164°12'09.3"E)	KF366664	KF366662
<i>Dierogekko nehoueensis</i>	AMS R162976	Rivière Néhoulé (21°25'03"S, 164°13'15"E)	JF972437	JF972425
<i>Dierogekko nehoueensis</i>	AMS R161242	Dôme de Tiébaghi (20°27'38"S, 164°11'11"E)	KF366665	JF972424
<i>Dierogekko poumensis</i>	AMS R166981	Sommet Poum (20°14'19"S, 164°01'56"E)	–	JF972398
<i>Dierogekko poumensis</i>	MCZ R184132	Sommet Poum (20°14'19"S, 164°01'56"E)	–	JF972399
<i>Dierogekko poumensis</i>	AMS R175535	Sommet Poum (20°15'0.8"S, 164°01'24.2"E)	JF972446	–
<i>Dierogekko poumensis</i>	AMS R175536	Sommet Poum (20°15'0.8"S, 164°01'24.2"E)	JF972443	JF972401
<i>Dierogekko poumensis</i>	AMS R175537	Sommet Poum (20°14'52.6"S, 164°01'23.3"E)	JF972447	JF972402
<i>Dierogekko poumensis</i>	AMS R161203	Sommet Poum (20°15'44"S, 164°02'07"E)	JF972444	JF972400
<i>Dierogekko poumensis</i>	AMS R161204	Sommet Poum (20°15'44"S, 164°02'07"E)	JF972445	–
<i>Dierogekko poumensis</i>	AMS R161205	Sommet Poum (20°15'44"S, 164°02'07"E)	JX024375	–
<i>Dierogekko baaba</i> , n. sp.	MNHN 2010.0621	Île Baaba (20°04'22"S, 163°57'05"E)	JF972457	JF972409
<i>Dierogekko thomaswhitei</i>	AMS R161153	Gomen Mine, Mt. Taom (20°46'36"S, 164°33'45"E)	JX024376	JF972420
<i>Dierogekko thomaswhitei</i>	AMS R161154	Gomen Mine, Mt. Taom (20°46'36"S, 164°33'45"E)	JF972450	JF972417
<i>Dierogekko thomaswhitei</i>	AMS R161178	Mt. Taom (20°46'36"S, 164°33'45"E)	–	JF972419
<i>Dierogekko thomaswhitei</i>	AMS R164183	Massif d'Ouazangou-Taom (20°46'55"S, 164°34'53"E)	JF972448	–
<i>Dierogekko thomaswhitei</i>	AMS R164186	Massif d'Ouazangou-Taom (20°46'50"S, 164°35'00"E)	JF972449	–
<i>Dierogekko thomaswhitei</i>	MNHN 2004.0018	Massif d'Ouazangou-Taom (20°46'40"S, 164°34'38"E)	–	JF972418
<i>Dierogekko validiclavis</i>	AMS R144230	Mt. Panié (20°33'35"S, 164°47'03"E)	JF972461	JF972415
<i>Dierogekko validiclavis</i>	AMS R149305	Mt. Panié (20°33'35"S, 164°47'03"E)	KF366668	JF972416
<i>Dierogekko validiclavis</i>	AMS R153695	Mt. Mandjélia (20°33'35"S, 164°31'06"E)	KF366669	–
<i>Dierogekko validiclavis</i>	AMS R153696	Mt. Mandjélia (20°33'35"S, 164°31'06"E)	JF972460	–

CODON POSITION	MODEL
ND2 1st	TVM + G
ND2 2nd	HKY + I + G
ND2 3rd	GTR + G
tRNAs	TVM + G
KIF24 1st	TrN + I
KIF24 2nd	TrN + I
KIF24 3rd	K81uf + I

TABLE 2

Codon positions and evolutionary models for the gene fragments used in this study.

SYSTEMATIC PART

RESULTS

Family DIPLODACTYLIDAE Underwood, 1954

Genus *DIEROGEKKO* Bauer, Jackman, Sadlier & Whitaker, 2006

Type species. *Dierogekko validiclavis* (Sadlier, 1989).

Dierogekko inexpectatus Bauer, Jackman, Sadlier & Whitaker, 2006

MORPHOLOGY — Eighteen specimens of *Dierogekko inexpectatus* were captured at Paevala, Sommet Poum (20°14'55.0" S, 164°01'21.9" E) by A. H. Whitaker and V. A. Whitaker on 23 and 27 September, 2006. Of these, eight specimens were preserved (AMS R045135-39, 23.IX.2006, AMS R045144-46, 27.IX.2006), providing additional morphological data on the species. The new specimens agree well in most aspects of morphology to the holotype (MNHN 2004.0025) and range in size from 31.7 to 39.5 mm (Table 3). Two specimens, CAS 248153 and AMS R175531, have only a single internasal, but the remaining specimens have two. This contrasts with three, as recorded in the holotype. There were four males among the sample, of which pore data could be collected for three. All have two uninterrupted rows of precloacal pores, with a longer anterior row (11-13 pores) and a shorter posterior row (7-8 pores). There is also variation in dorsal pattern. Although CAS 248154 and AMS R175527-30 are similar to the holotype, with a distinct striped pattern, CAS 248152-53 and AMS R175531 lack paired whitish stripes and instead exhibit two parallel rows of 11 small, pale cream-colored dots with irregular thin dark brown ventral and posterior borders running from the occiput to the sacrum (Figure 3). The vertebral area enclosed by these rows of dots is similar to the remaining dorsal coloration. The striped and spotted color morphs occur in roughly equal proportion and are not correlated with age or sex.

DISTRIBUTION AND NATURAL HISTORY — The habitat at the new site for *D. inexpectatus* is generally similar to the type locality, comprising a dense, closed-canopy forest (Figure 4) growing on a cuirasse surface with deep boulder beds (Figure 5), although the canopy is somewhat lower (~5-6 m *versus* >10 m) and trunk diameters smaller (to ~30 cm *versus* ~45 cm). Both the type locality and the new site for *D. inexpectatus* are on the northern end of the Sommet Poum plateau at 300-330 m elevation. Both sites are in tiny remnants of closed forest (approximately 0.9 ha and 0.5 ha, respectively). Four additional remnants of similar forest habitat occur in the same vicinity, together totalling just over 0.5 ha (0.06-0.18 ha), but surveys in these —and in less comparable forest remnants elsewhere on the Poum massif— have failed to detect *D. inexpectatus*, although *D. poumensis* was

TABLE 3

Mensural data specimens of *Dierogekko inexpectatus*. Abbreviations as in Materials and methods. All measurements in mm.

	MNHN 2004.0025	CAS 248152	CAS 248153	CAS 248154	AMS R175527	AMS R175528	AMS R175529	AMS R175530	AMS R175531	AMS R167252
HOLOTYPE										
Sex	female	Male	Female	Female	Male	Male	Male	Female	Female	Female
SVL	39.5	38.2	38.3	38.8	38.3	38.2	36.4	39.5	31.7	37.2
ForealL	4.9	4.9	4.8	4.6	4.7	4.7	4.9	4.8	4.2	4.3
CrusL	5.7	5.7	5.5	5.7	5.6	5.8	5.8	5.6	5.1	5.4
TailL	36.2	21.7	24.6	4.4 (br)	4.4 (br)	3.9 (br)	25.6	3.7 (br)	33.8	23.9
(regen.)	(25.8)	(12.4)	(4.2)	—	—	—	(20.4)	—	—	(19.5)
TailW	4.8	4.4	4.6	—	—	—	4.4	—	3.4	3.3
TrunkL	17.4	17.3	16.1	18.1	17.0	17.7	16.7	17.4	14.4	16.7
HeadL	10.5	10.1	9.9	9.7	10.0	9.8	10.1	9.8	9.1	9.3
HeadW	7.2	7.4	7.1	7.4	7.4	7.0	7.2	7.3	6.6	6.0
HeadH	4.1	4.1	4.5	4.5	4.6	4.4	4.5	4.7	3.3	3.3
OrbD	2.5	2.7	2.5	2.4	2.5	2.9	2.5	2.6	2.2	2.4
EyeEar	3.0	2.9	2.6	2.6	2.9	3.1	3.0	2.9	2.5	2.5
SnEye	4.6	4.7	4.7	4.1	4.8	4.5	4.3	4.1	3.0	3.5
NarEye	3.0	2.8	2.9	2.9	2.9	3.0	3.0	2.8	2.4	2.5
Interorb	3.5	3.6	3.4	3.7	3.4	3.8	3.8	3.6	2.9	3.0
EarL	1.4	1.5	1.3	1.4	1.4	1.6	1.4	1.1	1.0	1.1
Internar	1.3	1.3	1.6	1.2	1.3	1.6	1.4	1.5	1.2	1.3
Internasals	3	2	1	2	2	1-2	2	2	1	1
PreClPores	—	11/7	—	—	13/7	?	11/8	—	—	—
Pattern	stripes	dots	dots	stripes	stripes	stripes	stripes	stripes	dots	dots

present in all but one of them (Whitaker & Whitaker 2007a 2008). The presence of ancient stumps and logs and the unmistakably seral nature of much of the present maquis vegetation clearly indicate that the forest remnants are the last surviving fragments of what had presumably been a more or less continuous forest cover across on the entire cuirasse plateau (*ca.* 76 ha) before being destroyed, primarily by wildfires. The remaining forest remnants have been damaged by prospecting activities (cut by bulldozed tracks) and are subject to on-going degradation from browsing by deer (*Cervus timorensis*).

As with the discovery of the type specimen, at the new location *D. inexpectatus* was found during the day ($n = 11$) only beneath laterite boulders on the forest floor, generally deep down between the stones and the underlying soil. Examination of loose bark and holes and crevices in trees failed to find any *D. inexpectatus* in retreat sites above the ground. At night *D. inexpectatus* ($n = 7$) was found foraging on the foliage or fine terminal twigs of subcanopy shrubs, 0.8–1.6 m above ground.

Dierogekko inexpectatus has not been recorded at the type locality since the original specimen was collected in 2001 but it appears to be locally common at the new site. During daytime searches eight individuals were found in one boulder pile of $\sim 6 \text{ m}^2$ and a further three at a similar site nearby that was $\sim 9 \text{ m}^2$. The *D. inexpectatus* detected while active at night were found at an encounter rate of 2.7/person hour.

The boulder piles occupied by *Dierogekko inexpectatus* are also inhabited by *Kanakysaurus viviparus*. *Dierogekko poumensis* and *Eurydactylodes agricolae* are syntopic with *D. inexpectatus* in the foliage at night. Our limited data indicate that the smaller congener, *D. poumensis*, is less numerous but *E. agricolae* occurs in approximately equal numbers to *D. inexpectatus*. *Caledoniscincus atropunctatus* was the only other lizard species recorded within the forest remnants. *Dierogekko poumensis* and *E. agricolae* are abundant in the maquis shrublands that immediately surround the forest remnants inhabited by *D. inexpectatus*; other species present are *Hemidactylus frenatus*, *H. garnotii*, *Caledoniscincus haplorhinus*, *C. atropunctatus*, *C. austrocaledonicus*, *Kanakysaurus viviparus*, *Lioscincus nigrofasciatus* and *Phoboscincus garnieri*. *Oedodera* aff. *marmorata* and *Cryptoblepharus novocaledonicus* occur elsewhere on the summit of the massif.



FIGURE 3

Striped and dotted color morphs of *Dierogecko inexpectatus*.

CONSERVATION STATUS — The additional survey work and new data confirm that the provisional conservation status of Critically Endangered for *D. inexpectatus* (Bauer *et al.* 2006) is appropriate. The species has only ever been recorded at two sites which together give an extent of occurrence of approximately 5.0 ha and area of occupancy of 1.4 ha. Although it appeared to be relatively common at one of these sites in 2007, the small extent of the available habitat means the total population of *D. inexpectatus* is presumably very low. Its continued occurrence at the type locality is in doubt, as it has not been seen there since 2001. The habitat at both sites is vulnerable to the wildfires that frequently affect the Poum massif (the most recent on the plateau burnt ~11 ha of maquis shrubland in about 2002 pers. observ.) and is threatened with continued degradation by deer.

Trap data revealed that the introduced rats *Rattus exulans* and *R. rattus* are abundant on Sommet Poum, as are feral cats, and both rats and cats are serious predators of lizards. Although no direct evidence of predation on *D. inexpectatus* was obtained, cat droppings were found to contain lizard bones. Introduced little red fire ants (*Wasmannia auropunctata*) have invaded the type locality since 2001 and are now abundant in all forest remnants. It is not known if they are implicated in the apparent disappearance of *D. inexpectatus* from the type locality but there is no question that fire ants have a serious detrimental impact on lizard populations, including the local extirpation of some species (Jourdan *et al.* 2000, 2001). The introduced yellow crazy ant (*Anoplolepis gracilipes*) is also now widespread in maquis and forest remnants on the plateau and northern slopes of the Poum massif (Julien Le Breton, pers. comm., 9 June 2007) and it, too, is known to adversely impact lizard biodiversity and population density.

At some time between 2001 and 2006 *Hemidactylus frenatus* invaded the plateau area and is now common in the maquis shrublands and along the forest margins (it has not yet been recorded within the closed forest). This highly-invasive



FIGURE 4

View to the south across closed forest habitat at the type locality of *Dierogecko inexpectatus* at Paevala, Poum massif, Province Nord, New Caledonia.

and aggressive, introduced species is known to displace indigenous gecko taxa through competition for retreat sites and food resources, and by preying on small geckos, and in extreme cases has even resulted in local extinctions (e.g., Bolger & Case 1992; Case *et al.* 1994; Petren & Case 1996; Brown *et al.* 2002; Cole *et al.* 2005).

However, the overwhelming threat to the survival of *D. inexpectatus* is from the planned expansion of the nickel mine on Sommet Poup. Current proposals are that the entire plateau area will be mined over a 15-20 year period and this would see the removal of all vegetation from the cuirasse surface, including the closed forest remnants occupied by *D. inexpectatus*.

Although quantitative data on population size and trends are lacking for *D. inexpectatus*, the species' extremely restricted range (one location, <5 ha), the threats to its habitat (mining, wildfires, browsing ungulates, invasive weeds), the presence of mammalian predators (rats, cats), and the impacts of fire ants, yellow crazy ants and *Hemidactylus frenatus*, mean *Dierogekko inexpectatus* is assessed as Critically Endangered (A3c; B1a, b[iii, v]; B2a, b[iii, v]) (IUCN 2001), and the impact of these threats could drive the small population from which this species is known to extinction within the very near future.

MOLECULAR PHYLOGENETICS — There were 399 variable and 343 parsimony informative sites for ND2, 118 variable and 88 parsimony informative sites for the tRNAs, and 72 variable and 37 parsimony informative sites for KIF24. The ND2 data for the expanded data set retrieves the same topology as reported by Bauer *et al.* (2006) for relationships within *Dierogekko*, again with generally high support values for some interspecific relationships (Figure 6). The additional *D. inexpectatus* sequences are nearly identical to that obtained from the single individual available in 2006 and as in the previous study, this species is part of a clade including *D. validiclavis* and *D. nehoueensis*. The single *Dierogekko* from Île Baaba (AMS R 167252)



FIGURE 5

Cuirasse boulder piles inhabited by *D. inexpectatus* at Paevale, Poup massif, Province Nord, New Caledonia.

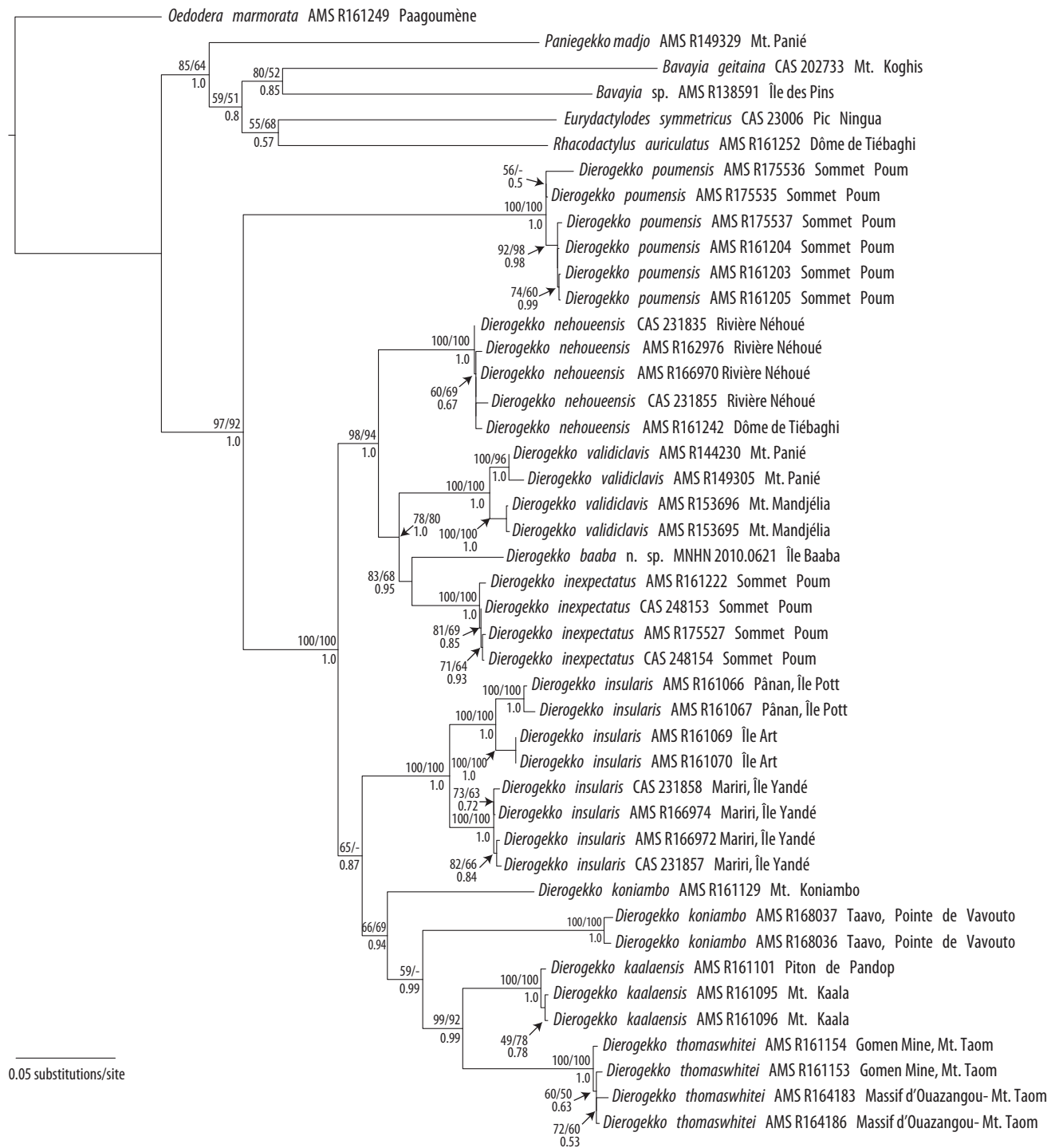


FIGURE 6

Maximum likelihood tree based on a fragment of the mitochondrial gene ND2 showing relationships among species of *Dierogekko*. Values subtending branches are maximum likelihood/maximum parsimony bootstrap values above the line and Bayesian posterior probabilities below the line.

is sister to *D. inexpectatus* within this clade, but without significant branch support. The clade comprising *D. insularis*, *D. thomaswhitei*, *D. kaalaensis*, and *D. koniambo* receives only moderate support, although the sister group relationship between *D. thomaswhitei* and *D. kaalaensis* is well-supported under all three analytical approaches. *Dierogekko koniambo* from Pointe de Vavouto do not cluster with those from Mt. Koniambo and this taxon is thus paraphyletic in both the likelihood and Bayesian analyses, although it receives some support as a natural group under parsimony; pending further investigation we regard the two populations as separate conservation units.

KIF24 (tree not shown), with its limited number of variable sites also retrieves a monophyletic *Dierogekko* and places *D. poumensis* as sister to the remaining taxa, although the latter with low support (ML bootstrap 70%; BI pP 0.90). Interspecific relationships among the remaining taxa are not generally well-supported and are based on only 35 variable sites, only 17 of which are informative, although a clade including *D. validiclavis*, *D. kaalaensis*, *D. thomaswhitei*, as well as the specimen from Baaba, had a posterior probability of 0.97.

The genetic distinctiveness of the Île Baaba specimen (ND2 uncorrected p-distance: 5.9708–14.8278 %, Tajima-Nei distance: 6.3411–17.016 % divergent from its congeners), along with several distinctive morphological features, support its recognition as a new species, which we describe here:

Dierogekko baaba Bauer, Whitaker & Sadlier, n. sp.

Figure 7

TYPE MATERIAL — Holotype: MNHN 2010.0621 (formerly AMS R 167252): Adult female; New Caledonia, Province Nord, Île Baaba, 0.35 km SW Pucet Manaat, 20°04' 10.9"S, 163°57' 18.7"E (elevation 15 m a.s.l.), collected by A.H. Whitaker and V.A. Whitaker, 24 June 2006.

ETYMOLOGY — The species name *baaba* is a noun in apposition referring to the type locality of this form on Île Baaba.

TABLE 4

Comparison between species of *Dierogekko*.

TAXON	MAX. SVL (MM)	PRECLOACAL PORE ROWS	DISTAL SUBDIGITAL SCANSORS	DORSAL COLORATION
<i>D. baaba</i> n. sp.	37.2	?	divided, narrow	pale vertebral region; thin dorsolateral stripes and pale dots weakly developed
<i>D. inexpectatus</i>	39.5	2 (11–13/7–8)	divided	dorsolateral stripes bold, or replaced with parallel rows of spots; no dark vertebral stripe; venter yellow
<i>D. insularis</i> (Yandé)	40.0	1 (12)	divided	vertebral region variably contrasting with flanks; dorsolateral stripes bold, or replaced with parallel rows of spots
<i>D. insularis</i> (Beleps)	41.4	2 (9–12/1–8)	divided	
<i>D. kaalaensis</i>	45.4	1 (12–15)	divided	pale vertebral region variably contrasting with flanks; thin dorsolateral stripes variably developed
<i>D. koniambo</i>	43.0	1 (10–12)	divided	pale vertebral region variably contrasting with flanks; dorsolateral stripes and dots absent on trunk
<i>D. nehoueensis</i>	40.3	2 (12/5–8)	divided	dorsolateral stripes bold or replaced with parallel rows of spots
<i>D. poumensis</i>	38.3	1 (8–11)	undivided	bright white dorsolateral stripes over sacrum and tail base, weakly contrasting on trunk; dark vertebral stripe present, sometimes indistinct; venter gray
<i>D. thomaswhitei</i>	44.9	2 (12–14/1–5)	divided	vertebral region weakly contrasting with flanks; dorsolateral stripes absent or vague
<i>D. validiclavis</i>	45.0	2 (12–16/8–11)	divided	pale vertebral region; thin dorsolateral stripes variably developed or replaced with parallel rows of spots

DIAGNOSIS — *Dierogecko baaba* can be distinguished from all congeners on the basis of the following combination of characters: size relatively small (37.2 mm in unique type), one internasal scale; subdigital lamellae relatively narrow, divided distally; [male preanal pore condition unknown]. Dorsum with a broad, pale vertebral stripe with edges weakly demarcated by vague pale dots and thin, broken dark borders. In addition to those features noted in Table 4, *D. baaba* can be distinguished from its congeners by its narrower digits (compare Figures 3 and 7).

DESCRIPTION — *Adult female*. (Holotype) SVL 37.2 mm; TailL 23.9 mm (distal 19.5 mm regenerated). Head short (HeadL/SVL ratio 0.25), wide (HeadW/HeadL ratio 0.65), depressed (HeadH/HeadL ratio 0.35), weakly set off from relatively thick neck. Loreal region without inflated canthal area; interorbital region neither concave nor convex. Snout relatively short (SnEye/HeadL ratio 0.38), blunt; longer than eye diameter (OrbD/SnEye ratio 0.66); scales on snout and forehead small, rounded, granular to weakly conical, homogeneous; scales on snout much larger than those on occipital region. Eye relatively large (OrbD/HeadL ratio 0.24); pupil vertical with crenelated margins; supraciliaries short, bearing three elongate spines near posterodorsal margin of orbit. Ear opening elliptical, angled posterodorsally at an angle of 45° from horizontal, large (EarL/HeadL ratio 0.12); eye to ear distance less than diameter of eyes (EyeEar/OrbD ratio 0.87). Rostral wider (1.6 mm) than deep (0.9 mm), incompletely divided dorsally. Two moderately enlarged supranasals separated by a single heptagonal internasal approximately same size as supranasals. Rostral in contact with first supralabials, nostrils, supranasals and internasal. Nostrils rounded, each surrounded by supranasal, rostral, first supralabial, nasal and 3 (right) or 4 (left) postnasals. At least four rows of small scales separate orbit from supralabials. Mental triangular, approximately as wide as deep (1.0 mm). A single enlarged (~8 times size of granular throat scales) hexagonal postmental, anterior apex narrowest, bordered by mental, first infralabials, and four enlarged chin shields, two posteriorly and one each posterolaterally. Two to three scale rows posterior to postmental and medial to infralabials enlarged relative to remainder of chin and throat scales. Supralabials to midorbital position 8/8; total enlarged supralabials 9/9; supralabial scales to angle of jaws 14/14. Enlarged infralabials 8/8; infralabials to angle of jaws 12/12. Interorbital scale rows across narrowest point of frontal bone 15, 31 scale rows between supraciliary scale rows of left and right sides.

Body slender, elongate (TrunkL/SVL ratio 0.45) no ventrolateral folds. Dorsal scales smooth, granular to conical, homogeneous. Ventral scales larger than dorsals, smooth, hexagonal to oval and subimbricate to imbricate, roughly uniform in size across venter, slightly larger on posteriormost abdomen. Approximately 124 scale rows around midbody. Gular region with homogeneous, smooth granular scales, slightly larger than dorsal granules. No enlarged precloacal or femoral scales; no precloacal or femoral pores. No enlarged cloacal spurs.

Scales on palm and sole smooth, rounded to oval or subrectangular. Scallation on dorsal surfaces of limbs similar to body dorsum. Fore and hindlimbs short and thick (ForeaL/SVL ratio 0.12; CrusL/SVL ratio 0.15). Digits relatively weakly dilated; claws well developed and recurved on digits II-V; claw much reduced and less strongly recurved on digit I, situated between asymmetrical distal pads (lateral pad approximately twice size of medial). Basal subdigital lamellae broad, rectangular, becoming bowed distally and angled and divided beneath distal phalanges (except for terminal scansors). Scansors (terminal scansors of digit I not included in counts): 4-9-10-11-10 manus; 6-8-10-10-10 pes. Relative length of digits: IV>III>V>II>I (manus); IV>III~V>II>I (pes); interdigital webbing moderately well developed between all digits of manus and digits I-IV of pes. Regenerated tail shorter than SVL (TailL/SVL ratio 0.64), thick, slightly constricted at base, tapering sharply along distal 1/3. No caudal tubercles; dorsal caudal scales rectangular, juxtaposed to subimbricate, eight rows per tail segment; subcaudal scales larger than dorsals.

Coloration (in preservative). Dorsal ground color mid-brown, with a wide, beige vertebral stripe, approximately 20-24 scale rows wide, along entire trunk. Lateral margins of stripe with some discontinuous darker edging scales and two parallel rows of 11 vague pale dots from occiput to tail base. Scattered darker scales within the vertebral stripe, some forming vague transverse marks, especially on posterior trunk. Lower flanks light brown with scattered darker scales. Sacral region mostly pale with dark irregular central markings.

Crown of head and dorsum of snout pale, continuous with broad vertebral stripe. An asymmetrical dark marking along length of nasal region. A broad dark band from nostril to front of orbit and from posteroventral rim of orbit, above

ear, to join darker lateral trunk coloration. Labial scales mid- to dark brown with cream gaps often bracketing sutures between scales. Iris blackish.

Limbs mottled; palms, soles and subdigital surfaces brown. Regenerated portion of tail midbrown with irregular darker markings, some longitudinally oriented, especially distally. Venter beige with scattered small, dark punctations on individual scales, especially in precloacal region and along length of thighs; chin mottled. Tail venter light brown, with relatively uniform brown pigment flecks across all scales; scattered larger dark brown markings irregularly distributed. Venter of regenerated portion of tail becoming darker distally.

Coloration (in life). Pattern as in preserved specimen. Body dorsum pale grayish-brown, lateral surfaces brown with scattered darker brown speckling, transitioning to yellowish-brown near ventrolateral margins of trunk (Figure 7). Paravertebral spots pale ashy gray. Venter milky yellow. Limbs mottled purplish-brown. Tail dorsum yellowish-brown proximally, becoming grayish-brown distally, with scattered darker markings. Crown grayish-brown, loreal stripe chocolate brown, labial scales yellowish with scattered dark speckling. Iris a bright coppery beige.

DISTRIBUTION AND NATURAL HISTORY — The only known specimen was collected at night as it foraged in the crown of a maquis shrub approximately 2 m above ground. The site was at the foot of a steep, south-facing slope with very sparse, low-growing woody maquis on a bouldery, peridotite surface. The animal was found at the margin of taller (to 3 m), denser maquis paraforestier that bordered closed coastal forest on the valley floor.

Pucet Manaat (134 m) is the highest point on Île Baaba (2,100 ha) and the vicinity of this peak is the only part of the island on an ultramafic surface. The vegetation in this area comprises a mosaic of maquis and maquis paraforestier on the slopes, interspersed with varying areas of outcropping peridotite and bare eroding soil surfaces. There are small remnants of closed forest near the peak and patches of savannah grassland. A narrow strip of closed coastal forest borders the coast. The vegetation in this area has been highly modified by wildfires and is degraded by introduced deer, cattle and horses.



FIGURE 7
Life photograph
of holotype of
Dierogekko baaba n sp.
(MNHN 2010.0621)
illustrating color
pattern and the
relatively weakly
dilated toes.

It is highly likely that the range of *Dierogecko baaba* will be limited to the vicinity of Pucet Manaat (Figure 2). Six of the eight previously described *Dierogecko* species are confined to maquis shrubland and closed forest habitats on ultramafic surfaces, *D. nehoueensis* is almost entirely so (except for one population in adjacent gallery forest on alluvial river flats), and only *D. validiclavis* occurs in closed mesic forests on metamorphic surfaces (Bauer *et al.* 2006). If *D. baaba* is restricted to ultramafic habitats like most of its congeners the only part of Île Baaba with potential habitat is approximately 77 ha on Pucet Manaat and 23 ha on a hill 0.6 km to the south. The remainder of Île Baaba comprises sedimentary (schist) and alluvial surfaces covered almost entirely with savannah grassland and degraded secondary shrubland, with small, scattered, degraded remnants of closed forest and sclerophyll forest, mostly in the south. Surveys in some of these forest remnants, including one just 3.5 km E of Pucet Manaat, have failed to detect *Dierogecko* (Whitaker *et al.* 2004).

The very limited information on the ecology of *Dierogecko baaba* indicates that—in common with the other *Dierogecko* species—it probably uses retreat sites on the ground beneath stones and litter, and forages in the outer canopy twigs of maquis shrubs at night.

Dierogecko baaba is syntopic with an undescribed member of the *Bavayia cyclura* clade and sympatric with *Caledoniscincus haplorhinus*; other lizard species recorded on Île Baaba are *Lepidodactylus lugubris*, *Caledoniscincus atropunctatus*, *C. austrocaledonicus*, *Cryptoblepharus novocaledonicus* and *Lioscincus nigrofasciolatum* (Whitaker & Whitaker 2007b).

CONSERVATION STATUS—Only a single *Dierogecko baaba* was found in 11 hours of night-searching in maquis shrubland and forest margins, and none were found by day (Whitaker & Whitaker 2007a), suggesting the population density of this species in the vicinity of Pucet Manaat is very low. The habitat at this site is vulnerable to wildfires, and ongoing degradation by deer, cattle and horses has a further negative impact on the remaining habitat. Trap data revealed introduced rats (*Rattus rattus*) are abundant at this site and feral cats were also observed. Although both rats and cats are serious predators of lizards, no direct evidence of predation on *D. baaba* was obtained, but studies elsewhere on their impact on small lizards indicate they are likely to have a significant negative effect on the *D. baaba* population. Introduced little red fire ants (*Wasmannia auropunctata*) are also present on Île Baaba and are known to impact severely on lizard populations (Jourdan *et al.* 2000, 2001). Although there are no quantitative data on population size and trends, the species' extremely restricted range (one location, <100 ha), the threats to its habitat (wildfires, browsing ungulates, invasive weeds), the presence of mammalian predators (rats, cats), and the impacts of fire ants, mean *Dierogecko baaba* is assessed as Critically Endangered (B1a, b[iii, v]; B2a, b[iii, v]) (IUCN 2001).

DISCUSSION

The initial finding of two genetically distinct *Dierogecko* sympatric on Sommet Poupou was unexpected given nearly all other taxa in the genus have allopatric distributions. The level of genetic differentiation between the two taxa was supported to some extent (given *D. inexpectatus* was represented by a single specimen) by morphological differences, and on this basis (Bauer *et al.* 2006) recognised as two distinct species, *D. poumensis* and *D. inexpectatus*. Subsequent field studies on Sommet Poupou have yielded additional specimens of *D. inexpectatus*, providing additional genetic and morphological data confirming the validity of the species. Further, extensive field surveys in northern Grande Terre (Whitaker & Whitaker 2007a,b, 2008), have failed to locate the species outside of Sommet Poupou, and it appears to be restricted to the small remnant forest patches near Paévala on Sommet Poupou. Examination of the additional specimens of *D. inexpectatus* show a level of variation in scalation and color pattern comparable to that seen in other species (Figure 3), even on the very limited spatial scale of Sommet Poupou. Of particular significance is the confirmation of the male precloacal pore pattern. A double row of precloacal pores is shared by *D. inexpectatus*, *D. thomaswhitei*, *D. validiclavis*, and *D. nehoueensis*, whereas a single row characterizes *D. poumensis*, *D. kaalaensis*, and *D. koniambo*. *Dierogecko insularis* can have one or two rows of pores, and the newly described *D. baaba* is known only from a female, and thus the condition of this character is unknown.

Differences in body size, scensor morphology, and coloration pattern in combination will allow most specimens of *Dierogecko* (Table 4) to be assigned to a particular species, although given the allopatric distribution of most species location

information alone will determine all species except *D. poumensis* and *D. inexpectatus*. These two species are among the most morphologically divergent members of the genus and are readily differentiated by differences in body size, precloacal pore row number, and subdigital morphology, and several obvious color pattern differences. All *D. inexpectatus*, whether striped or spotted, lack a mid-dorsal stripe but a narrow, darker, mid-dorsal stripe is invariably present in *D. poumensis*, albeit often indistinctly (Figure 1). Further, in life all *D. inexpectatus* have yellow ventral surfaces (including the throat), clearly distinguishing them from *D. poumensis* which has a gray ventral surface (Figure 8).

The discovery of a new species in the genus from the far northern islands, *Dierogekko baaba*, is not surprising, given the extent of microendemism of *Dierogekko* spp. on ultramafic surfaces from the Koniambo Massif north to the Îles Belep. Nonetheless, the relatively deep divergence between this species and its congeners is perhaps unexpected, given the lesser divergence between the more distant island populations of *Dierogekko* on Yandé and the Beleps currently assigned to *D. insularis*. The extremely small distributions of most *Dierogekko* suggest both that additional species may yet be discovered in remnant habitats in the Province Nord. As a consequence of their restricted range and the diverse array of threats they face certain members of the genus must be considered among the most critically endangered of all New Caledonian vertebrates. The presence of introduced mammals and geckos, as well as invasive ants and non-native vegetation severely compromises many *Dierogekko*, especially *D. inexpectatus* and *D. baaba*, with ranges apparently restricted to just a few hectares. Combined with the threat of periodic fires and potential catastrophic habitat damage through mineral extraction, these species are truly at the brink of extinction. We strongly support proactive measures to stabilize the remaining habitat of both *D. inexpectatus* and *D. baaba* to decrease risk levels to these species. Possible mechanisms include limits on mining in critical habitats and eradication of feral and invasive organisms like those implemented successfully in New Zealand (Townsend *et al.* 1997; Townsend & Broome 2003). Whitaker *et al.* (2004) suggested such eradication programs for Île Yandé, Île Art, and Île Pott, where *D. insularis* occurs, but Île Baaba could also be a candidate, although its proximity to the New Caledonian mainland may make rat recolonization inevitable.

FIGURE 8
Comparison of series of freshly euthanized *D. poumensis* (left) and *D. inexpectatus* (right) illustrating the grayish venter in the former and yellowish venter in the latter.



ACKNOWLEDGMENTS

We are grateful to the Province Nord authorities for supporting our herpetological research in northwestern New Caledonia. Our fieldwork was carried out under Convention de Collaboration N°. 80/2001 from the Direction du Développement Économique et de l'Environnement of the Assemblée de la Province Nord, and the majority of specimens of *Dierogekko* were collected under permits N°. 31 and N°. 49/02/SFE to Whitaker Consultants and permit N°. 01/03/COLL-SCE to Aaron M. Bauer. We particularly thank Joseph Manauté, Christian Papineau, Jean-Jérôme Cassan and Van Duong Dang and the staff at the Antenne DDEE de Koumac. For permission to visit various massifs and island localities, and for assistance, we are grateful to Claude Paquet of Société Minière du Sud Pacifique. Logistical support and encouragement was provided by Hervé Jourdan of IRD Nouméa and Vivienne Whitaker participated in all the fieldwork. This research was supported by grants DEB 0108108 and DEB 0515909 from the National Science Foundation (U.S.A.) to A. M. Bauer and T. Jackman and by the project BIONEOCAL funded by the Agence Nationale de la Recherche (France).

REFERENCES

- BAUER A. M., JACKMANT., SADLER R. A. & WHITAKER A. H. 2006 — A revision of the *Bavayia validiclavus* group (Squamata: Gekkota: Diplodactylidae), a clade of New Caledonian geckos exhibiting microendemism. *Proceedings of the California Academy of Sciences* 57: 503-547.
- BOLGER D. T. & CASE T. J. 1992 — Intra-specific and inter-specific interference behaviour among sexual and asexual geckos. *Animal Behaviour* 44: 21-30.
- BROWN S. G., LEBRUN R., YAMASAKI J. & ISHII-THOENE D. 2002 — Indirect competition between a resident unisexual and an invading bisexual gecko. *Behaviour* 139: 1161-1173.
- CASE T. J., BOLGER D. T. & PETREN K. 1994 — Invasions and competitive displacement among house geckos in the tropical Pacific. *Ecology* 75: 464-477.
- COLE N. C., JONES C. G. & HARRIS S. 2005 — The need for enemy-free space: the impact of an invasive gecko on island endemics. *Biological Conservation* 125: 467-474.
- DRUMMOND A., ASHTON B., CHEUNG M., HELED J., KEARSE M., MOIR R., STONES-HAVAS S., THIERER T. & WILSON A. 2006 — Genious v4.7. *Biomatters Ltd.*
- HUELSENBECK J. P. & RONQUIST F. 2001 — MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754-755.
- IUCN 2001 — *IUCN Red List categories: Version 3.1*. IUCN Species Survival Commission, Gland, Switzerland & Cambridge, UK. 26 p.
- JOURDAN H., SADLER R. A. & BAUER A. M. 2000 — Premières observations sur les conséquences de l'invasion de *Wasmannia auropunctata* 1863 (Roger) sur les prédateurs supérieurs dans les écosystèmes néo-calédoniens. *Actes des Colloques Insectes Sociaux* 13: 121-126.
- JOURDAN H., SADLER R. A. & BAUER A. M. 2001 — Little fire ant invasion (*Wasmannia auropunctata*) as a threat to New Caledonian lizards: evidences from the sclerophyll forest (Hymenoptera: Formicidae). *Sociobiology* 38: 283-301.
- MADDISON D. R. & MADDISON W. P. 2008 — MacClade 4.08. Sunderland, MA. Sinauer Associates, Inc.
- NYLANDER J. A. A., WILGENBUSCH J. C., WARREN D. L. & SWOFFORD D. L. 2008 — AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics* 24: 581-583.
- PETREN K. & CASE T. J. 1996 — An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* 77: 118-132.
- POSADA D. & CRANDALL K. A. 1998 — Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817-818.
- STAMATAKIS A. 2006 — RAxML-VI-HP: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688-2690.
- STAMATAKIS A., GOKER M. & GRIMM G. W. 2010 — Maximum Likelihood Analyses of 3,490 rbcL sequences: scalability of comprehensive inference versus group-specific taxon sampling. *Evolutionary Bioinformatics* 6: 73-90.
- STAMATAKIS A., LUDWIG T. & MEIER H. 2005 — RAxML-III: a fast program for maximum likelihood-based inference of large phylogenetic trees. *Bioinformatics* 21: 456-463.
- TOWNS D. & BROOME K. G. 2003 — From small Maria to massive Campbell: forty years of rat eradication from New Zealand islands. *New Zealand Journal of Zoology* 30: 377-398.
- TOWNS D., SIMBERLOFF D. & ATKINSON I. A. E. 1997 — Restoration of New Zealand islands: redressing the effects of introduced species. *Pacific Conservation Biology* 3: 99-124.
- WHITAKER A. H., SADLER R. A., BAUER A. M. & WHITAKER V. A. 2004 — *Biodiversity and Conservation Status of Lizards in Threatened and Restricted Habitats of North-Western New Caledonia*. Report to Direction du Développement Économique et de l'Environnement, Province Nord, Koné, New Caledonia. Whitaker Consultants Limited, Motueka, New Zealand. vi + 105 p.
- WHITAKER A. H. & WHITAKER V. A. 2007a — *Survey of the lizard fauna of the Sommet Poum, Province Nord, New Caledonia*. Unpublished report to Société le Nickel-SLN, Nouméa, New Caledonia, from Whitaker Consultants Limited, Motueka, New Zealand. ii + 29 p.
- WHITAKER A. H. & WHITAKER V. A. 2007b — *Survey of the lizard faunas of selected sites in Province Nord, New Caledonia*. Unpublished report to Service de l'Environnement, Direction du Développement Économique et de l'Environnement, Province Nord, Koné, Nouvelle-Calédonie. Whitaker Consultants Limited, Motueka, New Zealand. iv + 24 p.
- WHITAKER A. H. & WHITAKER V. A. 2008 — *Extended survey for *Dierogekko inexpectatus*, Province Nord, New Caledonia*. Unpublished report to Société le Nickel, Nouméa, Nouvelle-Calédonie. Whitaker Consultants Limited, Motueka, New Zealand. ii + 24 p.

The New Caledonian Leopard Skink *Lacertoides pardalis* (Reptilia: Scincidae); a review of the species' morphology, distribution, behavior and conservation

Ross A. Sadlier ⁽¹⁾, Glenn M. Shea ⁽²⁾, Hervé Jourdan ⁽³⁾, †Anthony H. Whitaker ⁽⁴⁾ & Aaron M. Bauer ⁽⁵⁾

⁽¹⁾ Section of Herpetology, Australian Museum, 6 College Street, Sydney 2000, NSW, Australia
rosss@austmus.gov.au

^(1, 2) Faculty of Veterinary Science B01, University of Sydney, NSW 2006, Australia

⁽³⁾ Institut de Recherche pour le Développement, Laboratoire de Zoologie Appliquée - BPA5 98848 Nouméa Cedex / New Caledonia

⁽⁴⁾ Whitaker Consultants Limited, 270 Thorpe-Orinoco Road, Orinoco, RD1, Motueka 7196, New Zealand

⁽⁵⁾ Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA

ABSTRACT

Lacertoides pardalis is a large species of skink with uniquely small body scales, probably the smallest of any skink species in relation to its size. It was described in 1997 from two specimens from a single site in the far south of New Caledonia. Since the original description more than a decade ago a number of additional specimens (ranging from juveniles to large adults) have been collected in the region and these specimens in combination with field observations have provided new information on the species' biology, most notable of which are a live-bearing mode of reproduction, and insights into its trophic ecology. Stomach analysis indicates an omnivorous diet with saurivory of other skink species, predation of various invertebrates, and an unexpectedly high prevalence of frugivory, indicating this species may play an important role in seed dispersal. This is the first record of this ecological trait in the New Caledonian scincid lizard fauna. The new records also represent significant extensions in the range of the species, and confirm a preference for habitat in areas of outcropping peridotite rock set in low maquis shrubland. The area from which *Lacertoides pardalis* was initially described has changed dramatically during the period since its discovery, primarily from activities associated with the establishment of facilities and infrastructure throughout southern New Caledonia, particularly those to support the recently established and extensive nickel mining operation on the Goro Plateau. Because the species is still only known from a limited number of locations, one of which is in close proximity to mining operations, the species has been listed as 'Vulnerable' under IUCN criteria. Further work on the detailed ecology and biology of the species are required to better manage the populations of this species in the wild.

SADLIER R. A., SHEA G. M., JOURDAN H., WHITAKER A. H. & BAUER A. M. 2014 — The New Caledonian Leopard Skink *Lacertoides pardalis* (Reptilia: Scincidae); a review of the species' morphology, distribution, behavior and conservation, in GUILBERT É., ROBILLARD T., JOURDAN H. & GRANDCOLAS P. (eds), *Zoologia Neocaledonica 8. Biodiversity studies in New Caledonia*. Muséum national d'Histoire naturelle, Paris: 31-44 (Mémoires du Muséum national d'Histoire naturelle; 206). ISBN: 978-2-85653-707-7.

RÉSUMÉ

Le scinque léopard de Nouvelle-Calédonie *Lacertoides pardalis* (Reptile : Scincidae), une revue de la morphologie, de la distribution, du comportement et de la conservation de l'espèce.

Lacertoides pardalis est un scinque endémique de grande taille, caractérisé par de petites écailles sur tout le corps. Cette espèce a été décrite pour la première fois en 1997, à partir de 2 spécimens en provenance d'un unique site de récolte, dans l'extrême sud de la Grande Terre. Depuis la description originale, il y a une dizaine d'année, plusieurs individus ont été capturés dans la même région (des juvéniles mais également des spécimens adultes de grande taille). Ces captures permettent de fournir des informations sur la biologie et l'écologie de l'espèce, en particulier, une reproduction vivipare et un régime alimentaire généraliste, reposant sur de la prédation d'invertébrés mais également sur d'autres espèces de reptiles et de façon plus inattendue avec une frugivorie importante. *L. pardalis* pourrait jouer un rôle important pour la dissémination de certaines espèces du maquis, voire de lisières forestières. Ces nouvelles captures ont permis d'élargir significativement l'aire de répartition connue de l'espèce, qui est considéré vulnérable (VU) selon les critères de la liste rouge de l'IUCN. Cependant, la région d'où est connue *L. pardalis* a subi de profondes transformations au cours de la dernière décennie, en raison du développement de projet minier sur le plateau de Goro. Des études complémentaires restent à mener pour conserver cette espèce originale et unique des habitats de maquis rocheux du sud de la Nouvelle-Calédonie.

INTRODUCTION

New Caledonia has an extremely rich lizard fauna composed entirely of skinks (Scincidae, 50 species), gekkonid geckos (Gekkonidae, 6 species) and Southwest Pacific geckos (Diplodactylidae, 35 species). On a species per area basis this richness greatly exceeds that of larger Pacific islands including New Zealand. Equally as remarkable is the exceptionally high level of regional and localized endemism. All genera and species of Southwest Pacific geckos and all but three species of skinks are in genera endemic to the region, and the level of species richness will only increase as further new species and genera await description in both groups. By contrast there are few Pan-Pacific lizard taxa present in New Caledonia, and all but one of the gekkonid geckos found there are species with widespread distributions throughout the Pacific region (Bauer & Henle 1994), and most may be the result of human introduction (Grant-Mackay *et al.* 2004; Kennedy 2001).

Our recent studies have revealed an exceptional degree of endemism concentrated on the territory's ultramafic surfaces, areas which extend as a near-continuous block over much of the southern third of the island and as a series of near-coastal massifs scattered along its west side. The southern and western ultramafic areas have each been identified as a distinct biogeographic region for lizards (Bauer & Sadlier 2000; Bauer *et al.* 2006a; Sadlier *et al.* 2009), each with a number of endemic lizard species (Bauer *et al.* 2006a, 2006b, 2012; Sadlier *et al.* 2004, 2006, 2009, 2013, 2014a, 2014b). Today the vegetation over much of these ultramafic ranges is dominated by maquis, a low heath-like shrubland that extends from low to high elevation. In contrast humid forest on the ultramafics is now usually present as remnant patches of varying size surrounded by maquis habitat, although large areas of forest occur in the high rainfall areas of the southeast ranges. Prior to the arrival of humans humid forest is thought to have been more extensive and that much of the existing maquis formations seen today are secondary and largely the result of extensive and repeated firing (McCoy *et al.* 1999; Perry & Enright 2002), both pre- and post- European settlement. Humid forest is characterized by a high level of lizard species richness, reflecting the diversity of niches within this habitat, and probably also its carrying capacity in terms of the biomass and diversity of invertebrates available as food (Jourdan & Sadlier pers. comm.) By contrast the lizard fauna of maquis shrubland tends to be less species-rich, and in the southern region is considered to be depauperate (Bauer & Sadlier 2000). The only truly maquis-dependant species of skinks are the sister taxa *Lioscincus tillieri* (Sadlier & Bauer, 1999) and *Lioscincus maruia* (Sadlier *et al.* 1998) which occupy the ultramafic surfaces of the southern and central ranges respectively, and *Lacertoides pardalis* a species known only from ranges in the far south of the island (Sadlier *et al.* 1997). In the central-west/north-west region ranges a number of species in the recently described diplodactylid gecko genus *Dierokekko* also appear to show a high level of reliance on maquis habitat (Bauer *et al.* 2006a), as does the recently described skink *Lioscincus vivae* (Whitaker *et al.* 2004), but it is not known yet, whether these taxa are strictly confined to this habitat.

The southern ultramafic region species *Lacertoides pardalis* was described from specimens collected on Kwa Néie in the far south of the Grande Terre in 1995, at a road cutting through maquis shrubland with extensive outcroppings of low

rock on lateritic soil (Sadlier *et al.* 1997). At the time it was assumed to show a degree of reliance on this particular type of habitat, which on the Goro Plateau was noted as being restricted to the vicinity of the Kwa Néie range and adjoining Monts Nengoné. In the 15 years since its discovery the Kwa Néie site has been visited several times during the course of general field surveys in the area (Sadlier & Shea 2004, 2006; Sadlier 2009) and additional samples of *Lacertoides pardalis* have been obtained from this site. Further, survey work in other areas of southern New Caledonia has resulted in the discovery of several other populations (Sadlier & Jourdan 2010; Whitaker Consultants, unpublished survey results), increasing significantly the potential area of occupancy for the species and confirming the original assumptions regarding the species preference for maquis habitat associated with areas of outcropping peridotite. Over this time we have opportunistically collected further samples that have provided additional data on aspects of the morphology and biology of the species that we report here. Also, tissue samples from this material have allowed a preliminary assessment of the degree of inter-population genetic variation across the species' range. Our additional field research in the area has also allowed us to more accurately assess the species' potential distribution in the region, and the threats posed by current and proposed mining and development activities in the region (Pascal *et al.* 2008).

MATERIALS AND METHODS

SYSTEMATICS

Institutional prefixes for the specimen referenced are as follows: AMS - Australian Museum, Sydney; CAS - California Academy of Sciences, San Francisco; MNHN - Muséum national d'Histoire naturelle, Paris.

The characters used in the re-description of *Lacertoides pardalis* were derived as follows: Measurements: snout to vent length - measured from tip of snout to caudal edge of anal scales; axilla to groin distance - measured from middle of base of the forelimb to middle of base of hindlimb; forelimb to snout length - measured from tip of snout to middle of base of forelimb; hindlimb length - measured from middle of base of hindlimb to tip of fourth toe including nail; tail length - measured from caudal edge of anal scales to tip of tail, on complete original tails only. Body measurements are expressed as percentages of snout to vent length (SVL) in the taxon accounts. Scalation: Head scalation follows Sadlier (2010). For characters used in the re-description abbreviation is given in parentheses: midbody scale rows (MBR) - number of longitudinal scale rows around body counted midway between axilla and groin; dorsal scale rows (DSR) - number of scales in a row from first scale posterior to parietal scale to last scale at the level of vent opening; fourth finger (FFS) and toe (FTS) scales - number of dorsal scales on fourth digit of hand and foot, distal scale contains claw and basal scale broadly contacts adjacent basal scale of third finger or toe; fourth finger (FFL) and toe (FTL) lamellae - number of ventral scales on fourth digit of hand and foot, distal scale contains claw and basal scale is last largely undivided scale at a point level with intersection of third and fourth digits. Bilaterally scoreable scalation characters were counted on both sides and the mean value used; in the holotype description these values are presented as left/right values.

The number of presacral and postsacral vertebrae (complete original tails only) were determined from radiographs prepared using a Eresco AS2 X-ray machine at exposures of 30 sec at 30 kV.

Polarities for morphological characters(*) follow Sadlier (2010).

GENETIC DATA

We obtained sequence data from a 514 bp fragment of the mitochondrial NADH dehydrogenase 2 (ND2) gene from nine samples from three of the four known locations for *Lacertoides pardalis* and the outgroups used are those from broader phylogenetic studies on New Caledonian skinks (Smith *et al.* 2007) and sequences for these were obtained from Genbank (Appendix 1). Protocols and analyses follow those outlined in Sadlier *et al.* (2012a, 2012b).

DIETARY ANALYSIS

Faecal material and gut contents were stored in 70% alcohol and analyzed under a dissecting microscope. Due to the digested nature of the material examined, invertebrates could only be identified to order or family level. Reptilian remains were identified to species by comparison of scales present in samples with a reference collection. Plant materials were also identified to family or genera using comparison with herbarium specimens from the IRD Herbarium.

SYSTEMATIC PART

Lacertoides pardalis Sadlier, Shea & Bauer, 1997

Figure 1

Lacertoides pardalis Sadlier, Shea & Bauer, 1997: 381.

TYPE MATERIAL — AMS R.148050 (holotype) and MNHN 1996.2662 (paratype) both originally cited as from Kwa Néie, collected by R. Sadlier & G. Shea 28 September 1995.

The species was described from two individuals collected on Kwa Néie in 1995. Since its description a further 10 specimens of *Lacertoides pardalis* have been obtained from sites across southern New Caledonia. These specimens have provided considerably more information on morphological and genetic variation within the species. Character states marked with an asterisk are those that in combination diagnose *Lacertoides* from all other genera in the *Eugongylus* group of skinks.

MATERIAL EXAMINED — The species is redescribed from 3 sub-adult males (95, 76 & 75 mm SVL), 4 adult females (102–131 mm SVL) and 2 subadult females (81 mm SVL), and 3 juveniles (64–67 mm SVL).

DESCRIPTION — Tests for sexual dimorphism in scalation found no significance differences for the scalation characters surveyed.

Measurements (adults and subadults only). Distance from axilla to groin 50.8–65.4% SVL (mean = 56.4, n = 12); distance from forelimb to snout 34.8–41.8% SVL (mean = 38.7, n = 12); hindlimb length 44.7–53.1% SVL (mean = 49.5, n = 12); *tail length 197.0–217.3% SVL (mean = 209.7, n = 7).

Scalation (all specimens). Naris situated within a single nasal scale and with a prominent postnasal suture, rarely fused to form a crease; frontonasal broader than long, *divided anteriorly and laterally such that two additional elongate scales are present either side, and prevent contact with the adjacent nasal and rostral scale, one pair being positioned laterally and contacting the anterior loreal + nasal and the other pair being positioned anteriorly and contacting the nasal + rostral, with the two elements of the latter pair meeting medially above the rostral to exclude contact between with the frontonasal and rostral scales, on some individuals the elements of the anterior and lateral pairs of these scales fuse to the adjacent scales (Figure 2); prefrontals moderately large and in moderate contact medially; frontal longer than broad; supraoculars four; *frontoparietals fused; interparietal distinct; parietals large, distinct, and in narrow to point contact behind interparietal; nuchals usually *divided into two or more large scales; upper secondary temporal scale single; temporal scales on side of head fragmented, the homologies are difficult to discern in some cases but present as follows where the scales can be discerned with some confidence: primary temporal single or divided into two scales, secondary temporal usually divided to form two, occasionally three scales, rarely single, tertiary temporals two or three; postlabials two, occasionally three; nasals moderately to widely separated; supraciliaries usually 8 (58%), occasionally 7, rarely 9; upper labials usually *8 (75%) with the sixth subocular, occasionally 7 or 9; lower labials *7 or 8 (80%), rarely 6 or 9; upper labials separated from contacting the lower eyelid by a *complete subocular row of 9–12 scales; loreals two, each contacting the labials broadly; postmental contacting first and second lower labial; transversely enlarged chinshields three, first pair in broad contact,



FIGURE 1

Coloration of *Lacertoides pardalis*: (A) typical boldly marked adult from Montagne des Sources; (B) older more obscurely marked adult from Kwa Née.

second pair separated by two scales, *third pair divided such that five scales separate those scales bordering the labials either side; body scales smooth, and *extremely small; lower eyelid with an obvious, centrally-located, semi-transparent disc; midbody scale rows 67-77 (mean = 71.25, sd = 2.90); dorsal scale rows 139-158 (mean = 149.7, sd = 5.63); scales on top of fourth finger 14-17 (mean = 16.2, sd = 0.66); lamellae beneath fourth finger 19-23 (mean = 20.92, sd = 1.22); scales on top of fourth toe 21-26 (mean = 23.4, sd = 1.41); lamellae beneath fourth toe 30-37 (mean = 34.1, sd = 2.12).

Osteology. Presacral vertebrae 29; postsacral vertebrae 61 and 63 on the two juvenile specimens (CAS 205843 and AMS R.152644 respectively) both of which have complete tails, and 61 for the holotype (AMS R148050); premaxillary teeth *9.

Coloration. The species epithet (Sadlier *et al.* 1997) was assigned to emphasize the unique ocellated pattern on the body. It was based at the time on two specimens, one an adult female (holotype) the other a subadult male. Since then additional large specimens of both sexes have been obtained, as well as juveniles. No obvious sexual dimorphism in color or pattern was reported in the original description and there is none evident between the larger specimens of either sex collected since. What has been observed with the additional specimens collected is that the distinctiveness of the pattern of dark ocelli is reduced in the largest individuals (all females). Also, the single individual (an adult female) from high elevation habitat (840 m) on the plateau area of Montagne des Sources is darker in coloration overall, a trait often typical of high elevation populations of some skinks (pers. obs.), but observations of additional individuals are needed to determine whether this trend is consistent throughout the population.

COMMENTS — The ‘supranasal’ scale character originally described for *L. pardalis* requires amendment. The presence of supranasal scales in skinks was one of the primary characters used in assigning species to groups early in the history of skink systematics, but differences in the terminology and interpretation of head scalation characters have made its use in the diagnoses and descriptions by early workers difficult to follow, and subject to misinterpretation (Sadlier 2010). Greer (1974) in his assessment of the polarity of character states in skink systematics regarded the presence of supranasal scales as indicative of the ‘primitiveness’ of a taxon, and its loss as apomorphic. Within the *Eugongylus* group of skinks, of which *Lacertoides pardalis* is a member, this character has been re-examined across a range of taxa (Sadlier 2010) and found it to be highly variable in structure. This calls into question the utility of a simplistic presence vs absence in assigning polarity, and hence past perceptions of the presence of this character state as a common platform within the *Eugongylus* group from which shared derivations by fusion of the elements of the supposed supranasal were interpreted as evidence of relationship. In the light of the assessments made, large, well defined, and putatively homologous supranasal scales in the *Eugongylus* group occur only in *Eugongylus* (some taxa), *Emoia*, *Tachygia* and in the New Caledonian genus *Phoboscincus* (Sadlier 2010). The paired head scales in *Lacertoides pardalis* referred to as ‘supranasal’ scales by Sadlier *et al.* (1997) in the original

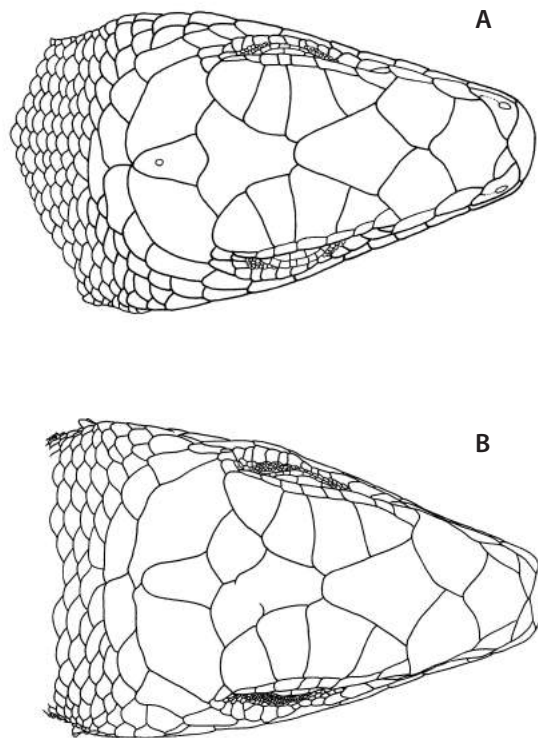


FIGURE 2

Dorsal head scalation of *Lacertoides pardalis*: (A) showing the condition in the holotype (AMS R.148050) and paratype (MNHN 1996.2662) in which the lateral pair of scales were absent and only the anterior pair (referred to as ‘supranasal’ scales in the original description) are present (fused to the nasal on the left side in the holotype); (B) the condition typical of most individuals in which fragmentation in the region of the frontonasal and nasal scales (AMS R.164376 - upper) has produced two additional scales either side.

description of the species are considered an independent derivation resulting from fragmentation in the region of the frontonasal and possibly nasal scales (Figure 2), and not homologous with the supranasal scales of *Phoboscincus* or *Eugongylus*.

POPULATION DIFFERENTIATION — Despite extensive survey work in southern New Caledonia in the past 10-15 years *Lacertoides pardalis* still remains known from only a few locations scattered across the region. In particular, extensive survey work on the Plaine des Lacs at a number of sites located between the Ka Yé Wagwé and Kwa Néie and across a range of habitat types, including extensive areas of maquis on the broken and outcropping lateritic cuirasse cap that characterizes much of the plateau, has failed to record the species. This would suggest the species is absent from intervening areas and has a fragmented distribution. However the genetic data available (Table 1) does not show a level of differentiation between populations consistent with long-term isolation of these populations from each other, rather the levels of within population differentiation are not markedly different from those between populations. We can only assume that despite its strong preferences for a particular habitat profile that is neither widespread nor continuous across the landscape, the species is capable of sufficient migration through intervening maquis shrubland to maintain gene exchange.

TABLE 1

Uncorrected pairwise distances based on a 514 bp fragment of the mitochondrial geneND2.

	1	2	3	4	5	6	7	8	9	10
1 <i>Lioscincus nigrofasciolum</i> AMS R.144361 Mt Dore										
2 <i>Lacertoides pardalis</i> CAS 205843 Kwa Néie	0.20 4									
3 <i>Lacertoides pardalis</i> AMS R148050 Kwa Néie	0.18 7	0.02 4								
4 <i>Lacertoides pardalis</i> AMS R.148051 Kwa Néie	0.18 7	0.02 4	0.00 3							
5 <i>Lacertoides pardalis</i> AMS R.164350 Kwa Néie	0.18 8	0.02 5	0.00 7	0.00 7						
6 <i>Lacertoides pardalis</i> AMS R.164376 Kwa Néie	0.18 6	0.02 5	0.00 1	0.00 1	0.00 5					
7 <i>Lacertoides pardalis</i> AMS R180299.001 Kwa Néie (Mine A1)	0.19 1	0.03 0	0.00 9	0.00 9	0.01 3	0.00 8				
8 <i>Lacertoides pardalis</i> AMS R.180300.001 Ka Yé Wagwé	0.18 7	0.02 4	0.00 3	0.00 3	0.00 4	0.00 1	0.00 9			
9 <i>Lacertoides pardalis</i> AMS R.167429 Ka Yé Wagwé	0.19 7	0.03 7	0.01 7	0.01 7	0.01 8	0.016 2	0.02 2	0.01 4		
10 <i>Lacertoides pardalis</i> AMS R.167430 Ka Yé Wagwé	0.19 5	0.03 3	0.01 2	0.01 2	0.01 3	0.01 0	0.01 8	0.00 9	0.02 1	
11 <i>Lacertoides pardalis</i> AMS R.174594 Montagne des Sources	0.184 9	0.03 9	0.02 1	0.02 1	0.02 2	0.02 0	0.02 7	0.01 8	0.03 0	0.02 7

DISCUSSION

The additional specimen records and observations acquired since the species' description in 1997 have not only extended its distribution more widely across the south of the island, but also provide important additional information on its biology, both of which have contributed significantly in a recent assessment of the species' conservation status (Whitaker & Sadlier 2011). Here we present a summary of that additional information.

DISTRIBUTION AND BEHAVIOR

The species has now been recorded four locations in southern New Caledonia (Figure 3):

- the plateau area at Montagne des Sources on the watershed between the Rivière Dumbéa and Rivière Blanche.
- Rivière Blanche in the Réserve naturelle terrestre de la Haute Yaté.
- Ka Yé Wagwé a large isolated range on the Plaine des Lacs in the vicinity of the Chutes de la Madeleine.
- the Kwa Néie in the far south of the region near the Baie de Prony.

Lacertoides pardalis has so far been recorded primarily from maquis habitat with outcropping rock (peridotite), predominately maquis shrubland, and one occasion from adjacent canopied maquis at the Rivière Blanche site. Comparative and more extensive searches of maquis shrubland on lateritic soils or cuirasse in the region have failed to record the species in that habitat, neither has it been recorded from areas of peridotite within humid forest.

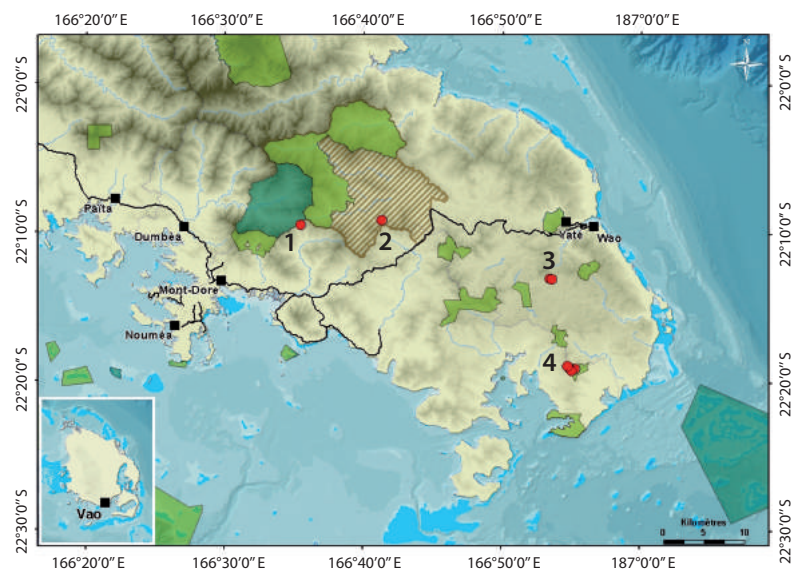
At Montagne des Sources the species was recorded at around 800 m elevation in the area of the Plateau des *Calliotropsis* (Figure 4A). A single individual was detected active in the middle of the day in the vicinity of a small isolated rock outcropping surrounded by low maquis shrubland; more extensive areas of outcropping rock were also scattered across the plateau. This site lies at the apex of the range that forms the watershed of the Dumbéa River on one side and the watershed of the Rivière Blanche on the other side.

At Rivière Blanche a single individual was recorded from outcropping rock at around 400 m elevation near the crest of the ridge in the vicinity of the ‘Houp Géant’, and another from adjacent canopied maquis paraforestier (Joël Delafenetre DENV – pers. comm.). The vegetation in this area comprises humid forest in the gullies but dense maquis elsewhere and on the crest of the ridge – a typical pattern for the lower ridges in this river valley.

Ka Yé Wagwé is a large, isolated east-west ridge on the north side of the Plaine des Lacs approximately 5 km in length and reaching a height of 200–330 m above the surrounding laterite plateau. There are some small patches of humid forest at its base but the range is covered by moderately-low dense maquis shrubland on the lower slopes and a low open maquis on the mid- to upper slopes. The range is unremarkable when viewed from the south, rising steeply but progressively to the crest at 500–630 m. However, it falls away abruptly on the northern side where the underlying peridotite forms a broken escarpment about 2 km long and with bluffs and cliffs 2–20 m in height (Figure 4B). Several adult individuals were observed in crevices within the more extensive areas of cliff and other individuals were detected among crevices on outcrops, and

FIGURE 3

Locations from which *Lacertoides pardalis* has been recorded in southern New Caledonia – solid circles are specimen records, hollow circles observations: 1) Montagne des Sources (AMS R.174594 22°08'17"S 166°35'55"E); 2) Rivière Blanche (obs. 22°09'03.1"S 166°41'40.2"E, obs. 22°09'04.9"S 166°41'38.4"E); 3) Ka Yé Wagwé (AMS R.167429 22°12'50.7"S 166°53'40.9"E; AMS R.167430 22°12'56.0"S 166°53'47.8"E); 4) Kwa Néie (AMS R.148050 22°18'48.3"S 166°54'58.7"E; MNHN 1996.2662, AMS R.152643–44, CAS 205843 22°18'51.9"S 166°55'06.7"E; AMS R.164350 & AMS R.164380 22°19'05"S 166°55'18"E; AMS R.164376 22°19'01"S 166°54'52"E; AMS R.166137 22°18'48.9"S.



a single subadult was also observed in a small area of outcropping rock on the top of the ridgeline away from the escarpment.

Kwa Néie is part of a series of connected ranges to the south of the Plaine des Lacs and separated from Ka Yé Wagwé by the extensive basin and accompanying wetlands of the lakes Lac en Huit and Grand Lac. The species has been recorded from a number of sites on Kwa Néie over the last 10 years. Most records are from searches made along the road to the transmitter tower that runs from a low saddle at ~280 m elevation to the summit of the range at ~490 m, primarily through the Réserve Naturelle Terrestre de la Forêt Nord. The track meanders up the north face of the range, passing initially through low (~1 m high), dense maquis shrubland near the crest of a low ridge (280-340 m) on which the underlying peridotite frequently surfaces, often as large exposed boulders (Figure 4C), but also on road embankments. It then passes through dense humid forest between 340-420 m, an area with extensive exposed peridotite at the surface, emerging into moderately low (~1-2 m tall) dense maquis shrubland on a steep slope near the summit (420-480 m), again with underlying peridotite frequently exposed as large outcrops. Six individuals have been recorded from exposed peridotite in cuttings where it passes through dense maquis between 280-340 m, and two from dense maquis shrubland in the area of the summit. A single adult individual has also been recorded from a crevice in rocks on the face of the track cutting where it passes through humid forest. This site was close to the interface between the

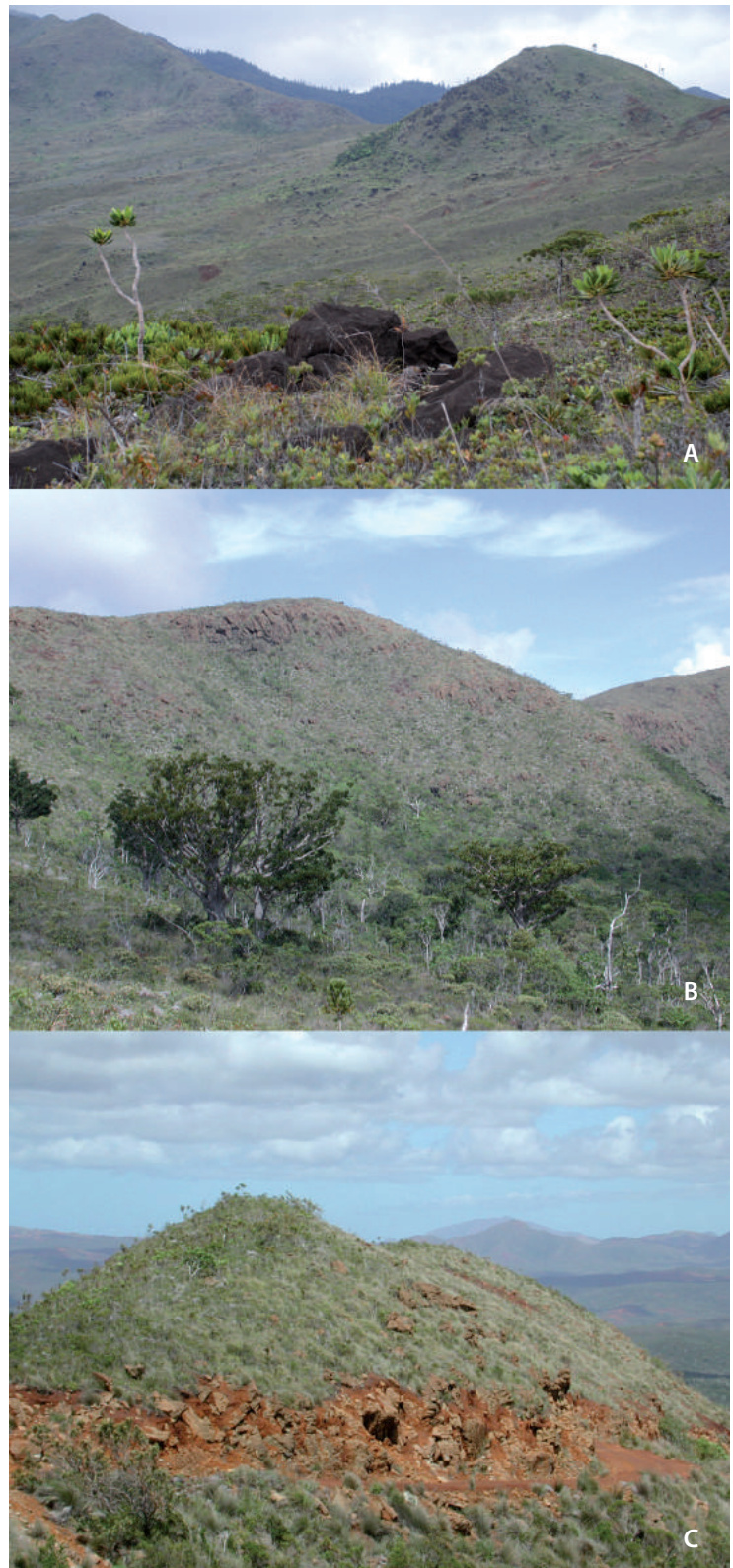


FIGURE 4

Habitat of *Lacertoides pardalis*: (A) isolated rock outcrop surrounded by low maquis shrubland at around 800m elevation on Montagne des Sources; (B) broken peridotite escarpment with bluffs and cliffs 2-20m in height near the summit of Ka Yé Wagwé; (C) dense maquis shrubland between 280-340m near the crest of the ridge on Kwa Néie near where the holotype was collected, note underlying peridotite present as large outcropping boulders.

humid forest and maquis shrubland at ~ 420 m, and the species' presence there is likely to be an artifact of the openness and continuity of rocky habitat offered by the track rather than an extension of its habitat preferences into humid forest, particularly given the close proximity of the adjacent maquis shrubland. A single large individual of *Lacertoides pardalis* has also been recorded from the southeast face of Kwa Néie in an area of mine concession comprising low maquis shrubland with extensive large peridotite boulders, where it was detected amongst crevices in an outcrop.

Lacertoides pardalis appears to be one of the most wary of the New Caledonian skinks. It has been disturbed or observed while active only on four occasions, and always at, or in close proximity to, a retreat site in or under rock. The majority of the remaining records are from individuals detected by strategically placed glue traps at the entrance to likely looking crevices in rocks. Several juveniles were detected along the transmitter tower track on Kwa Néie by turning exposed rocks embedded in soil in the road cutting, and the holotype from a shallow burrow in soil immediately beneath a large rock in the road cutting. Retreat sites included natural or partially excavated burrows in soil below rocks, and narrow crevices within outcropping rock or formed by rock on rock. While there is a clear preference for habitats that include rocky sites these can take the form of either, outcropping rock with a matrix of rock on rock, outcrops and rock faces with crevices, or in artificial situations such as road cuttings with large rocks embedded in a soil matrix – but only on exposed peridotite, not cuirasse, and predominately in maquis shrubland vegetation. These types of rock-dominated habitats tend to be situated mostly (but not always) near the crest of a ridgeline.

MATURITY AND REPRODUCTION

Lacertoides pardalis is one of the largest skinks in New Caledonia exceeded in size only by the two species of *Phoboscincus*. Despite living in tropical latitudes the species appears to have a typically temperate zone mode of reproduction that is strongly seasonal. The four largest individuals recorded (SVL 102–131 mm) are all females. The initiation of reproductive activity in adult females appears to be in the spring/early summer months (*i.e.* middle of the tropical dry season) with parturition in the mid-summer (*i.e.* late dry season/early wet season). Of the two large females collected in spring the largest (AMS R.174954 SVL 131 mm) collected in October was vitellogenic and carried 4 (1 left/3 right) very large yolked ovarian follicles, whereas the other (AMS R.148050 SVL 102 mm) collected in late September was mature but not reproductive. A large female (AMS R.164380 SVL 131 mm) collected in late December carried five (2 left/3 right) large oviductal yolk masses. No foetus was obvious but there was a vascular network over each of the large yolk masses indicating viviparity. Reproductive inactivity and quiescence in females likely occurs in the late summer/winter (*i.e.* wet/early dry season), as a mature female (AMS R.167429 SVL 134 mm) collected in February (early wet season) was non-reproductive, having only slightly (1/3) enlarged ovarian follicles. A small female (AMS R.167430 SVL 81 mm) collected February was immature and lacked enlarged or convoluted oviducts that would indicate reproductive activity in previous seasons.

The four largest males (75–95 mm) all have small testes with barely differentiated seminiferous tubules indicating they are reproductively immature. Three (AMS R.166137 SVL 76 mm, AMS R.164376 SVL 81 mm & R.164350 SVL 95 mm) were all collected mid-summer in late December (*i.e.* end of dry season). The single male (MNHN 1996.2662 SVL 75 mm) collected in the early spring/summer season (late September 1995) also had small testes, and if mature would have been expected to have enlarged testes at this time of year, suggesting immaturity at this size.

The three smallest individuals (AMS R.152643–44 & CAS 205843 SVL 64–67 mm) were all collected after summer in May (*i.e.* end of the wet season). Their size and the relative size of the developing clutch mass in the single gravid female carrying early term embryos would indicate that these juveniles were most likely the young from the previous year *i.e.* approximately 14–16 months old.

DIETARY HABITS

Dietary analyses were conducted on stomach contents from 7 adults and subadults, also one faecal sample was collected from a specimen that defaecated during handling. The frequency of various food items sorted from gut contents is given in Table 2.

Our study showed that *Lacertoides pardalis* are an omnivorous, generalist species, consuming a wide array of food types. At least 15 invertebrate groups were recorded, including earthworms, snails, spiders and insects (ants, bees, wasps, caterpillars, weevils - Table 2). The number of invertebrate prey items per stomach varied between 1-5. Some prey items (such as nitidulid beetles) may be secondary prey inadvertently ingested when fruit were being eaten. Amongst the invertebrates we also identified *Solenopsis geminata* (tropical red fire ant), an invasive ant that thrives in maquis areas, indicating a capability to adapt to new prey.

Stomach analysis also recorded body parts and scales of both young and adult *Caledoniscincus austrocaledonicus* on two occasions (Table 2), the first record saurivory for this species. *Lacertoides pardalis* is a large skink and as such could prey on a range of other lizards, particularly skinks. Saurivory in New Caledonian skinks has also been recorded for several other large species including *Caledoniscincus festivus*, *Lioscincus nigrofasciolatum*, and *Phoboscincus garnieri* (Jourdan et al., work in progress) and the gecko *Rhacodactylus auriculatus*, all of which have included *Caledoniscincus* spp. in their diet, indicating the common and widespread members of that genus could form an important opportunistic part of the diet of the lizard fauna.

The most significant find in the dietary analysis was a high prevalence of frugivory, with numerous seeds and fruit parts recorded (Table 2). The consumption of fruits was totally unexpected for a ground-dwelling skink in maquis shrubland (Bauer & DeVaney 1987, Shea *et al.* 2009). Seeds and fruits belonging to at least four shrub species in the Myrtaceae and Sapotaceae were found in five (70%) of the specimens examined. The high number of seeds ingested suggests *Lacertoides pardalis* may play a role in the dispersal of some plants in the maquis (such as *Uromyrtus* or *Leptostylis*), and possibly also for some typically forest species that are found on forest margins (such as *Planchonella*). This fruit consumption pattern may be seasonal (detailed phenology of the plants consumed should be investigated), but it may have a significance for maquis shrubland renewal and functioning. Fruit as a component of the diet has been recorded for the gecko *Rhacodactylus leachianus*, particularly on the offshore islands off the Isle of Pines (Aaron – references), but this is the first record of such dietary pattern in New Caledonian skink lizard fauna. Frugivory is commonplace in NZ skinks, including in similar sorts of habitats. In particular, *Oligosoma ottagense* (which is remarkably similar to *Lacertoides* in morphology, size, habitat and behavior) and *Oligosoma grande* which are both crevice inhabitants of rock outcrops in tussock/shrubland habitats, both consume very large quantities of fruits. Furthermore, they selectively feed on fruit at certain times of year, even though fruits of the same species are available at other times and invertebrates are uniformly available from spring to autumn. This preferential consumption of fruit is thought to indicate a special dietary need, probably in relation to the reproductive cycle.

During the dietary analysis we recorded a high parasite load (Nematoda) for most specimens (from 1 to 79 nematodes per stomach or pellet), with only 2 stomachs clear of nematodes. This high parasite load may be a consequence of predatory behavior on other skink species.

CONSERVATION STATUS

Lacertoides pardalis is present at only four locations, its extent of occurrence is approximately 24 km² and its area of occupancy is estimated to be <2 km². There are no quantitative data on population size and trends for the species but observations at the two sites, Kwa Néie, and Ka Yé Wagwé, indicate it occurs at low population density at both locations. *Lacertoides pardalis* was recently assessed as Vulnerable D2 using IUCN criteria (Whitaker & Sadlier 2011).

Our observations indicate *Lacertoides pardalis* is restricted to areas of outcropping peridotite rock set in low maquis shrubland. The distribution of such habitat in the Grande Sud is very restricted, and is most extensive on the crests of ranges where the underlying rock becomes exposed. As such, the potential habitat is likely to have a dendritic distribution that is fragmented, has a high edge to area ratio, and neither the extent of occurrence nor area of occupancy are likely to increase substantially, even with further records. The more extensive areas of the species preferred habitat occur on the crests of the ranges, and populations on the ridge tops are at risk from disturbance in the construction of access tracks, and from wildfires, which tend to increase in intensity as they move upslope. Further, these ridge tops are also the preferred

sites for wind powered electricity generators, the installation of which has expanded in the region in recent years, and results in extensive disturbance to the top of the ridges.

The species has now been recorded from three reserves in the Grand Sud and is considered to be well represented within the New Caledonian protected areas network. However, the Réserve Naturelle Terrestre de la Forêt Nord which includes part of the Kwa Néie population lies in close proximity to the industrial area and activities associated with the mining operations on the Goro Plateau. Within the context of the species' known distribution the population on Kwa Néie is one of the two largest and, although partly within a reserve, the close proximity to mining activities place this population in a vulnerable position. As such, the long-term conservation of *Lacertoides pardalis* would be greatly enhanced by the addition of Ka Yé Wagwé as a protected area within the provincial reserve system. The population on Ka Yé Wagwé is likely to be large by virtue of the extent of preferred habitat for the species along the crest of the range. Further, this area of habitat, which is dominated by exposed rock, is perhaps less likely to be affected by wildfires than other sites within the species' range. Further work on the detailed ecology and biology of the species are required to better manage the populations of this species in the wild.

TABLE 2

Dietary items. *one specimen of *Solenopsis geminata* and two specimens of *Pheidole* sp.

IDENTITY OF ITEMS			N° OF ITEMS	N° OF INDIVIDUALS
PLANTS				
Myrtaceae	Seeds	<i>Uromyrtus ngoyensis</i>	187	5
	Seeds	<i>Myrtastrum rufo-punctatum</i>	3	1
	Fruit parts	(<i>Uromyrtus</i> sp.)	2	2
Sapotaceae	Fruits	<i>Leptostylis (Pycnandra)</i> sp.	3	1
	Fruits	<i>Planchonella</i> sp.	1	1
Total plant items			196	
Plant items undet.	not fruit/seed			5
INVERTEBRATES				
Oligocheta			1	1
Gasteropoda			1	1
Arachnida	Acari Oribata		1	1
	Aranea	Undet.	1	1
Insecta	Coleoptera	Nitidulidae	1	1
		Curculionidae	1	1
		Cerambycidae	1	1
		Tenebrionidae	1	1
		Undet. larvae	1	1
		Undet. Caterpillar	1	1
		Chrysididae	1	1
		Megachilidae	1	1
		Sphecidae	3	2
		Formicidae*	4	2
	Psocoptera		1	1
Total invert. items			20	
Parasite load	Nematoda		119	5
VERTEBRATE				
	Scincidae	<i>C. austrocaledonicum</i>	2	2
	Skin shed			1

ACKNOWLEDGMENTS

The authors thank the New Caledonian authorities for their support in providing permits to collect and conduct field research in New Caledonia, in particular Anne-Claire Goarant (former Chef du Service des Milieux Terrestres, Direction de l'Environnement (DENV), Province Sud). Logistical support in Nouméa was provided by the Institut de Recherche pour le Développement (IRD), Nouméa. The occurrence of *Lacertoides pardalis* at Rivère Blanche is from records made by Joël Delafenetre, DENV Province Sud. The discovery of *Lacertoides pardalis* was made during survey work on the fauna of the Reserves of the Province Sud commissioned by the Direction de l'Environnement, Province Sud. The distribution map (Figure 3) was produced by Manina Tehei, Ingénieur Conservation Faune Vale Nouvelle-Calédonie. Special thanks are due to Stephane McCoy, botanist from Vale Nouvelle-Calédonie for his help in fruit and seed identification, and also Hervé Vandrot and Jérôme Munzinger from the Botany Section of IRD for identification of the Sapotaceae seed. Research commissioned by Vale-Nouvelle Calédonie around Forêt Nord contributed to the information presented here.

REFERENCES

- BAUER A.M. & DEVANEY K.D. 1987 — Comparative aspects of diet and habitat in some New Caledonian lizards. *Amphibia-Reptilia* 8: 349-364.
- BAUER A.M. & HENLE K. 1994. Das Tierreich 109 — Gekkonidae. Part 1, Australia and Oceania. Walter de Gruyter, Berlin. Xiii + 306 p.
- BAUER A.M. & SADLER R.A. 2000 — 'The Herpetofauna of New Caledonia'. (Society for the Study of Amphibians and Reptiles: Ithaca NY). 310 p, 24 pls.
- BAUER A.M., JACKMAN T., SADLER R.A. & WHITAKER A.H. 2006a — A revision of the *Bavayia validiclavis* group (Squamata: Gekkota), a clade of New Caledonian geckos exhibiting microendemism. *Proceedings of the California Academy of Sciences* 57(18): 503-547.
- BAUER A.M., JACKMAN T., SADLER R.A. & WHITAKER A.H. 2006b — A new genus and species of diplodactylid gecko (Reptilia: Squamata: Diplodactylidae) from northwestern New Caledonia. *Pacific Science* 60 (1): 125-135.
- BAUER A. M., SADLER R.A., JACKMAN T.R. & SHEA G.S. 2012 — A new member of the *Bavayia cyclura* species group (Reptilia: Squamata: Diplodactylidae) from the southeast ranges of New Caledonia. *Pacific Science* 66: 239-247.
- GRANT MACKIE J. A., BAUER A. M. & TYLER M.J. 2004 — Stratigraphy and herpetofauna of Mé Auré cave (site WMD007), Moindou, New Caledonia. *Cahiers Archéologiques* 15: 295-306.
- GREER A.E. 1974 — The generic relationships of the scincid lizard genus *Leiopisma* and its relatives. *Australian Journal of Zoology, Supplementary Series* 31:1-67.
- JAFFRÉ T. 2005 — Conservation programmes in New Caledonia, western Pacific: in place for the dry forest, but urgently needed for ultramafic vegetation. *BGjournal* 2(1): 13.
- JOURDAN H., SADLER R., BAUER A., 2001 — Little fire ant invasion (*Wasmannia auropunctata*) as a threat to New Caledonian Lizard: Evidences from a sclerophyll forest (Hymenoptera: Formicidae). *Sociobiology* 38(3): 283-301.
- KENNEDY A. 2011 — The fossil herpetofauna of the Pindai Caves, New Caledonia: with implications for the effect of human habitation on island faunas. M.Sc. Thesis, Villanova University, Pennsylvania, USA. 222 p.
- MCCOY S., JAFFRÉ T., RIGAUT F. & ASH J.E. 1999 — Fire and succession in the ultramafic maquis of New Caledonia. *Journal of Biogeography* 26: 579-594.
- PASCAL M., RICHER DE FORGES B., LEGUYADER H. & SIMBERLOFF D. 2008 — Mining and other threats to the New Caledonia biodiversity hotspot. *Conservation Biology* 22(2): 498-499.
- PERRY G.W. & ENRIGHT N.J. 2002 — Humans, fire and landscape pattern: understanding a maquis-forest complex, Mont Do, New Caledonia, using a spatial 'state-and-transition' model. *Journal of Biogeography* 29: 1143-1158.
- SADLER R.A. 2009 — Targeted survey for the rare regional endemic lizard *Lacertoides pardalis* at Forêt Nord, Prun. Unpublished report by Cygnet Surveys & Consultancy to Vale Inco Nouvelle-Calédonie. 14p.
- SADLER R.A. 2010 — Systematic studies of the scincid lizards of New Caledonia. PhD. Thesis, Griffith University, Queensland. 199 p.
- SADLER R.A. & BAUER A.M. 1999 — The scincid lizard *Lioscincus tillieri* (Reptilia: Scincidae) from New Caledonia in the southwest Pacific: new information on the species, biology, distribution, and morphology. *Records of the Australian Museum* 51(1): 93-98.
- SADLER R.A., BAUER A.M., WHITAKER A.H. & SMITH S.A. 2004 — Two new species of scincid lizards (Squamata) from the Massif de Kopéto, New Caledonia. *Proceedings of the California Academy of Sciences* 55(11): 208-221.
- SADLER R.A., BAUER A.M. & SMITH S.A. 2006 — A new species of *Nannoscincus* Günther (Squamata: Scincidae) from high elevation forest in southern New Caledonia. *Records of the Australian Museum* 58: 29-36.
- SADLER R.A., BAUER A.M., WOOD, P.L. JR., SMITH S.A. & JACKMAN T. 2013 — A new species of lizard in the genus *Caledoniscincus* (Reptilia: Scincidae) from southern New Caledonia and a review of *Caledoniscincus atropunctatus* (Roux). *Zootaxa* 3694 (6): 501-524.
- SADLER R.A., BAUER A.M., WOOD P.L., SMITH S.A., WHITAKER A.H., JOURDAN H. & JACKMAN T. 2014a — Localized endemism in the southern ultramafic bio-region of New Caledonia as evidenced by the scincid lizards in the genus *Sigaloseps* (Reptilia: Scincidae), with a description of four new species, in GUILBERT É., ROBILLARD T., JOURDAN H. & GRANDCOLAS P. (eds), *Zoologia Neocaledonica* 8. Biodiversity studies in New Caledonia. *Mémoires du Muséum national d'Histoire naturelle*, 206: 81-116.
- SADLER R.A., BAUER A. M., SMITH S.A., SHEA G.M. & WHITAKER A.H. 2014b — High elevation endemism on New Caledonia's ultramafic peaks - a new genus and two new species of scincid lizard, in GUILBERT É., ROBILLARD T., JOURDAN H. & GRANDCOLAS P. (eds), *Zoologia Neocaledonica* 8. Biodiversity studies in New Caledonia. *Mémoires du Muséum national d'Histoire naturelle*, 206: 117-128.
- SADLER R.A. & JOURDAN H. 2010 — Inventaire herpéologique des aires protégées de la province sud. Rapport de Convention DENV Province Sud, Convention n° 313.07 - Avenants ½. Nouméa. 27 p.

- SADLIER R.A., SHEA G.M., & BAUER A.M. 1997 — A new genus and species of lizard (Squamata, Scincidae) from New Caledonia, Southwest Pacific, in NAJT J. & MATILE L. (eds), *Zoologia Neocaledonica 4. Mémoires du Muséum national d'Histoire naturelle*, 171: 379-385.
- SADLIER R. & SHEA G. 2004 — Étude faunistique spécifique herpétofaune sur le site minier Goro Nickel proposé. Unpublished report to Goro Nickel S.A., Australian Museum Business Service, Sydney. 31 p.
- SADLIER R.A. & SHEA G.M. 2006 — Étude de l'herpétofaune de quatre réserves spéciales du grand sud de la Nouvelle Calédonie et propositions d'orientations de mesures de conservation - Réserve spéciale botanique Forêt Nord, Réserve spéciale botanique Cap N'Doua, Réserve spéciale botanique Pic du Pin, and Réserve spéciale botanique Pic du Grand Kaori. Unpublished report by AMBS to Direction des Ressources Naturelles, Province Sud, Noumea. 70 p.
- SADLIER R.A., SMITH S. A., BAUER A.M. & WHITAKER A.H. 2009 — Three new species of skink in the genus *Marmorosphax* SADLIER (Squamata: Scincidae) from New Caledonia, in GRANDCOLAS P. (ed.), *Zoologia Neocaledonica 7. Biodiversity studies in New Caledonia. Mémoires du Muséum national d'Histoire naturelle*, 198: 373-390.
- SADLIER R.A., WHITAKER A.H. & BAUER A.M. 1998 — *Lioscincus maruia*, a New Species of Lizard (Reptilia: Scincidae) from New Caledonia, Southwest Pacific. *Pacific Science* 52(4): 334-341.
- SHEA G., JOURDAN H., SADLIER R.A., BAUER A. 2009 — Natural history of the New Caledonian whiptailed skink *Tropidoscincus variabilis* (Bavay, 1869) (Squamata: Scincidae). *Amphibia-Reptilia* 30: 207-220
- SMITH S.A., SADLIER R.A. & BAUER A.M., AUSTIN C.C. & JACKMAN T. 2007 — Molecular phylogeny of the scincid lizards of New Caledonia and adjacent areas: Evidence for a Single Origin of the endemic skinks of Tasmantis. *Molecular Phylogenetics and Evolution* 43: 1151-1166.
- WHITAKER A.H. & SADLIER R.A. 2011 — *Lacertoides pardalis*, in IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>. Downloaded on 28 November 2011.
- WHITAKER A.H., SADLIER R.A., BAUER A.M. & WHITAKER V.A. 2004 — Biodiversity and Conservation Status of Lizards in Threatened and Restricted Habitats of North-Western New Caledonia. Report by Whitaker Consultants Limited to Direction du Développement Économique et de l'Environnement, Province Nord, Koné, New Caledonia. vi + 105 p.

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

Ross A. Sadlier⁽¹⁾, Aaron M. Bauer⁽²⁾, Perry L. Wood Jr.^(2,3)
Sarah A. Smith^(2,4), †Anthony H. Whitaker⁽⁵⁾ & Todd R. Jackman⁽²⁾

⁽¹⁾ Section of Herpetology, Australian Museum, 6 College Street, Sydney 2000, NSW, Australia
rosss@austmus.gov.au

⁽²⁾ Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA

⁽³⁾ Department of Biology and Bean Life Science Museum, Brigham Young University, Provo, UT, 84602, USA

⁽⁴⁾ Eco Logical Australia Pty Ltd., 16/56 Marina Boulevard Cullen Bay 0820, NT, Australia

⁽⁵⁾ Whitaker Consultants Limited, 270 Thorpe-Orinoco Road, Orinoco, RD1, Motueka 7196, New Zealand

ABSTRACT

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

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

RÉSUMÉ

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

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

INTRODUCTION

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

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

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

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

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

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

MATERIAL AND METHODS

SYSTEMATICS

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

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

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

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

GENETIC STUDIES

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

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

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

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

PHYLOGENETIC ANALYSES

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

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

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

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

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

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

RESULTS

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

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

TABLE 1

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

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

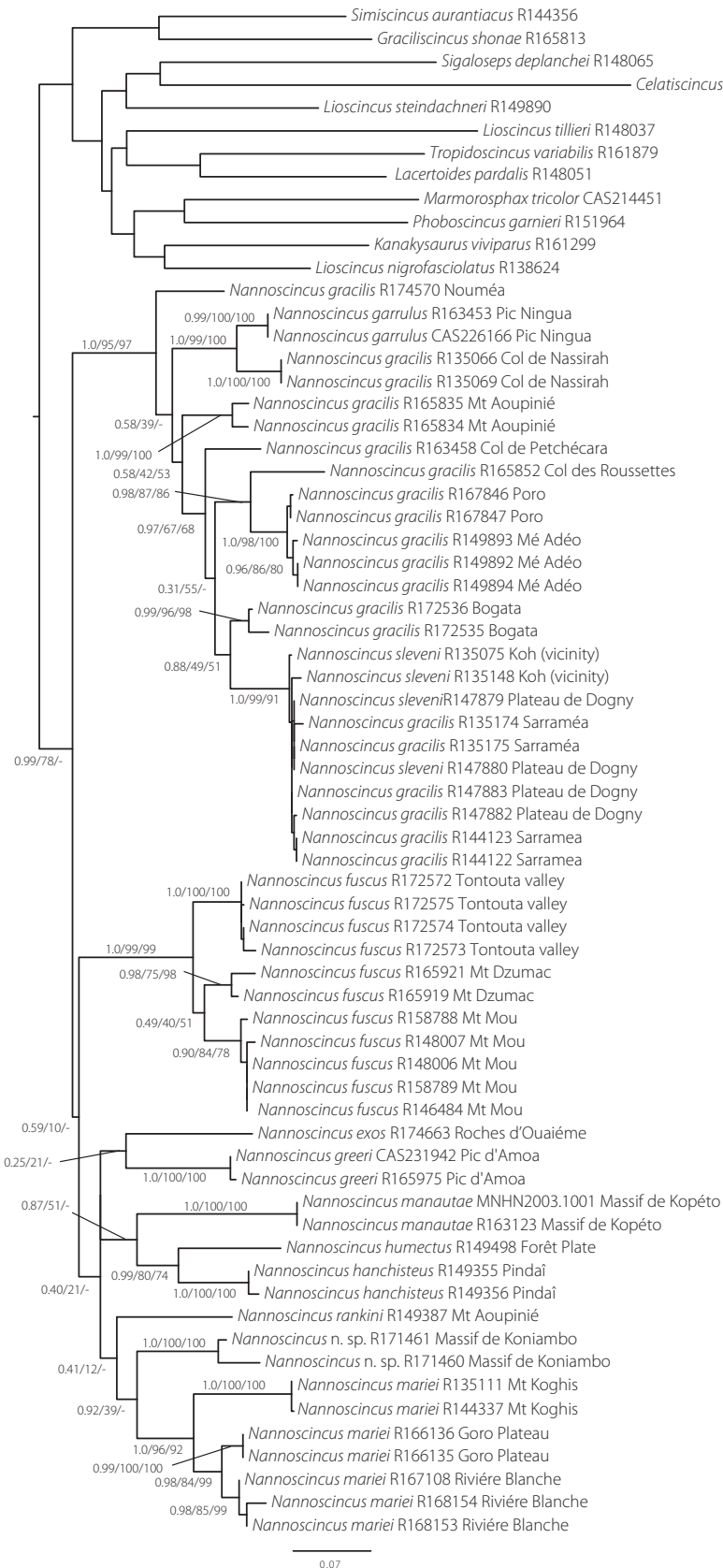


FIGURE 1

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

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

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

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

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

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

TABLE 2

Genetic distance between populations of *N. fuscus*.

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

TABLE 3

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

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

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

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

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

SYSTEMATIC PART

Family SCINCIDAE Gray, 1825

Genus *NANNOSCINCUS* Günther, 1872

Nannoscincus Günther, 1872: 472.

Type species. *Nannoscincus fuscus* Günther, 1872

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

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

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

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

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

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

***Nannoscincus mariei* (Bavay, 1869)**

Anotis mariei Bavay 1869: 29.

TYPE LOCALITY — New Caledonia.

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

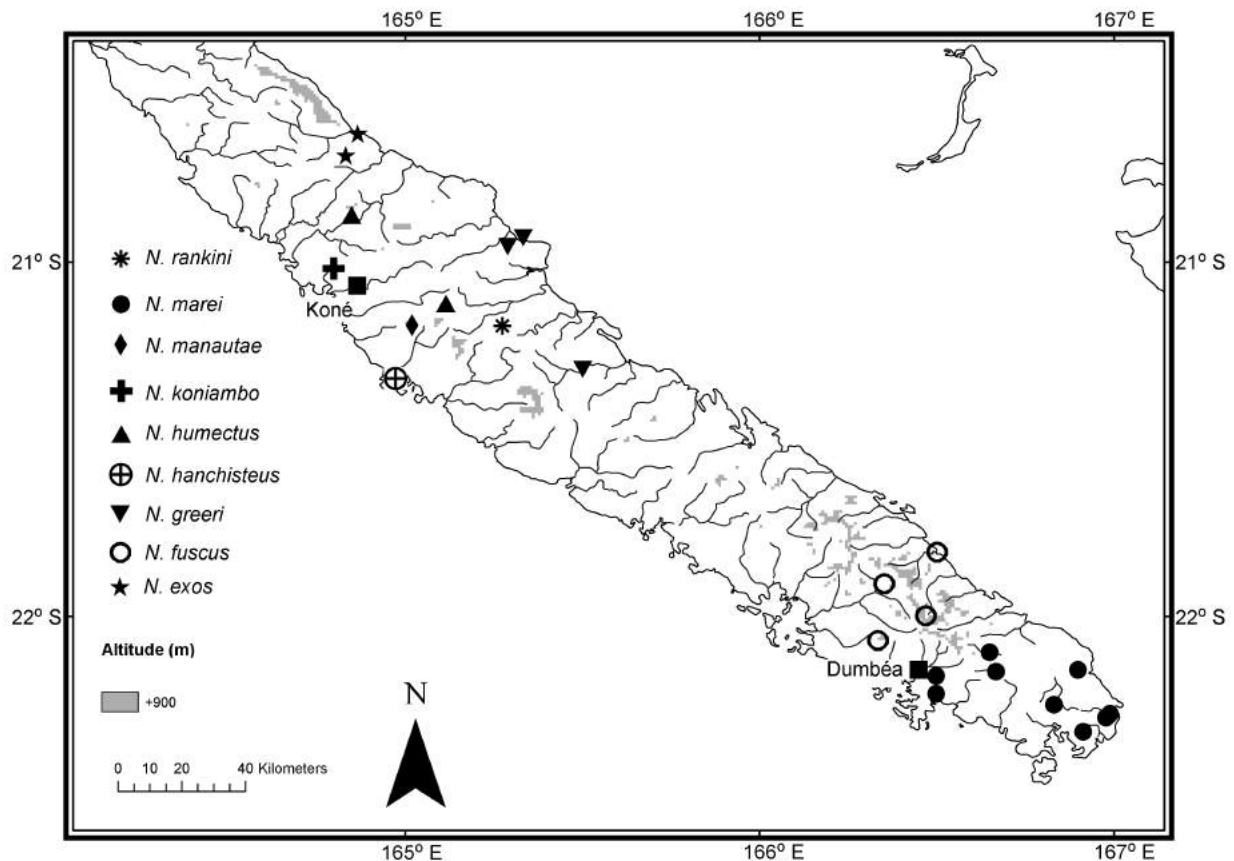


FIGURE 2
Distribution of the *N. 'mariei'* group in New Caledonia.

Nannoscincus gracilis (Bavay, 1869)

Lygosoma gracilis Bavay, 1869: 24

Mococa micropus Günther, 1872: 420

TYPE LOCALITY — New Caledonia (Figure 3).

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

Nannoscincus fuscus Günther, 1872

Nannoscincus fuscus Günther, 1872: 421.

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

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

Nannoscincus sleveni (Loveridge, 1941)

Lygosoma sleveni Loveridge 1941:193.

TYPE LOCALITY — Canala.

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

Nannoscincus rankini Sadlier, 1986

Nannoscincus rankini Sadlier, 1986: 62.

TYPE LOCALITY — Mt. Aoupinié.

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

Nannoscincus greeri Sadlier, 1986

Nannoscincus greeri Sadlier, 1986: 63.

TYPE LOCALITY — Mt. Koyaboa, Poindimié.

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

Nannoscincus humectus Sadlier, Bauer & Whitaker, 2002

Nannoscincus humectus Sadlier et al., 2002: 245

TYPE LOCALITY — Forêt Plate.

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

Nannoscincus hanchisteus Sadlier, Bauer & Whitaker, 2002

Nannoscincus hanchisteus Sadlier et al., 2002: 248

TYPE LOCALITY — Pindai.

DISTRIBUTION — North-west coast (Figure 2).

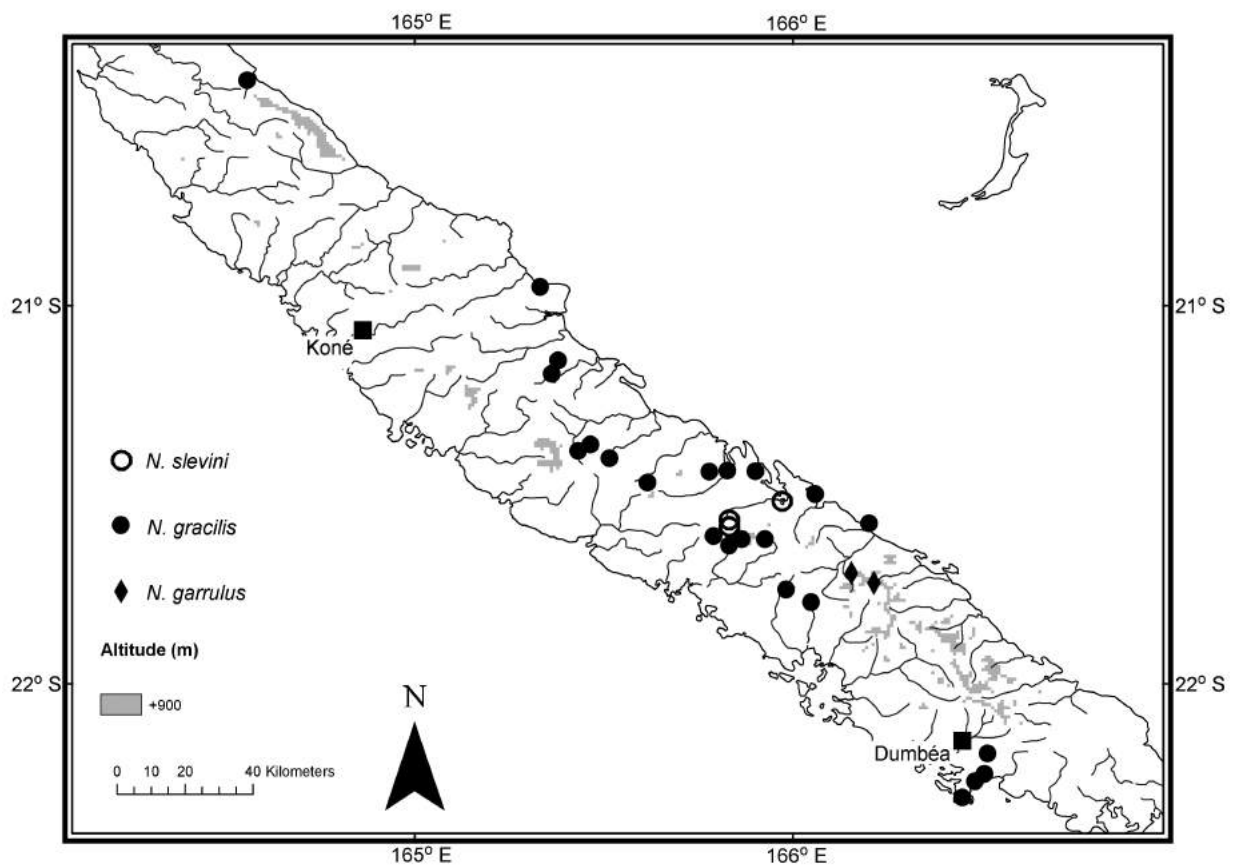


FIGURE 3
Distribution of the *N. 'gracilis' group* in New Caledonia.

Nannoscincus exos Sadlier, Bauer & Whitaker, 2002*Nannoscincus exos* Sadlier et al., 2002: 248**TYPE LOCALITY** — Roches de Ouiaème, 3 km west of Ouinguip.**DISTRIBUTION** — North-east region coastal ranges bounded by the Hienghène River valley in the south and the Ouaième River valley in the north (Figure 2).***Nannoscincus manautei*** Sadlier, Bauer, Whitaker & Smith, 2004*Nannoscincus manautei* Sadlier et al., 2004: 215**TYPE LOCALITY** — Massif de Kopéto, Papinda.**DISTRIBUTION** — Massif de Kopéto in the north-west ranges (Figure 2).***Nannoscincus garrulus*** Sadlier, Bauer & Smith, 2006*Nannoscincus garrulus* Sadlier et al., 2006: 31**TYPE LOCALITY** — Pic Ningua.**DISTRIBUTION** — Pic Ningua, Koungouhaou Nord and Mont Çidoa in the southern region ranges (Figure 3).***Nannoscincus koniambo*** Sadlier, Bauer, Wood & Whitaker, n. sp.**TYPE LOCALITY** — Massif de Koniambo.**DISTRIBUTION** — Massif de Koniambo in the north-west ranges.***Nannoscincus koniambo*** Sadlier, Bauer, Whitaker & Wood, n. sp.

Figures 4, 5

TYPE MATERIAL — **Holotype**. New Caledonia, MNHN 2011.0283 (formerly AMS R.171460) Massif de Koniambo, headwaters of Rivière Pandanus 20°59'40"S 164°48'41"E, 720 m (19 Jan. 2009; R. Sadlier).**Paratype**. AMS R.141461 Massif de Koniambo, headwaters of Creek Coco (south Branch) 20°58'32"S 164°47'50"E, 670 m (20 Jan. 2009; A. Whitaker).**ETYMOLOGY** — The epithet is a noun in apposition in reference to the type locality, the Massif de Koniambo. The content and order of authors for the description of the new species reflects the individual contributions of those individuals to the discovery and recognition of that species.

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

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

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

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



FIGURE 4

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

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

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

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

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

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

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

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

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



FIGURE 5

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

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

DISCUSSION

TAXONOMIC DISCUSSION

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

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

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

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

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

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

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

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

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

PHLOGEOGRAPHIC PATTERNS

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

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

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

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

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

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

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

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

ACKNOWLEDGMENTS

The specimens used in this research project have been collected over a long period time under a number of permits and we thank the authorities of Province Nord and Province Sud for permission to conduct our research. In particular, we thank the following individuals for their assistance with our research: Jean-Jérôme Cassan, Direction du Développement Économique et de l'Environnement (DDE-E), Province Nord; Anne-Claire Goarant (former Chef du service des milieux terrestres) and Joseph Manaute (Directeur Parc Provincial de la Rivière Bleue) Direction de l'Environnement de la Province Sud. The holotype of *Nannoscincus koniambo* was collected under permit No. 60912-355-2009/JJC issued by DDE-E. We gratefully acknowledge Koniambo Nickel (KNS) for commissioning the fieldwork and access to sites under their control, and the assistance of KNS staff, particularly Denis Poignonec (former Chef Service Système Environnemental). Some of the samples used in this research were collected during the course of field surveys of other mining leases and we gratefully acknowledge the assistance of the staff of Société Le Nickel (SLN) and Vale-Nouvelle Calédonie for access to sites under their control and in certain instances for commissioning the fieldwork. Hervé Jourdan of IRD Nouméa provided important logistical backing for our research in New Caledonia, and assistance from Vivienne Whitaker in many of the field surveys is gratefully acknowledged. Michael Elliot of the Collection Informatics Unit, Australian Museum produced the maps of distributions (Figures 2 & 3). Ivan Ineich of the Muséum national d'Histoire naturelle provided the French résumé. This research was supported by grants DEB 0108108 and 0844523 from the National Science Foundation (U.S.A.) to A. M. Bauer and T. Jackman and by the project BIONEOCAL funded by the Agence Nationale de la Recherche (France).

REFERENCES

- BAUER A. M. & SADLER R. A. 2000 — 'The Herpetofauna of New Caledonia'. Society for the Study of Amphibians and Reptiles, Ithaca NY, 310 p. + 24 pls.
- BAUER A. M., JONES J. P. G., & SADLER R. A. 2000 — A New High-Elevation *Bavayia* (Reptilia: Squamata: Diplodactylidae) from Northeastern New Caledonia. *Pacific Science* 54 (1): 63-69.
- BAVAY A. 1869 — Catalogue des reptiles de la Nouvelle-Calédonie et description d'espèces nouvelles. *Mémoires de la Société Linnéenne de Normandie* 15: 1-37.
- BOLLMER J. L., KIMBALL R. T., WHITEMAN N. K., SARASOLA J. H. & PARKER P. G. 2006 — Phylogeography of the Galápagos hawk (*Buteo galapagoensis*): A recent arrival to the Galápagos Islands. *Molecular Phylogenetics and Evolution* 39: 237-247.
- BOULENGER G. A. 1887 — Catalogue of the Lizards in the British Museum (Natural History), 2nd ed., vol. 3. British Museum (Natural History), London: 330.
- BRENCHLEY J. L. 1873 — Jottings during the Cruise of H. M. S. *Curaçoa* among the South Sea Islands in 1865. Longmans, Green, and Co., London. xxviii + 487 p., 52 pls, 1 map.
- BRYGOO E. R. 1985 — Les types de Scincidés (Reptiles, Sauriens) du Muséum national d'Histoire naturelle. *Zoologie, Biologie et Écologie animales* (4^e série), 7, (section A), n°3, Supplement: 1-126.
- CHAPPLED D. G., RITCHIE P. A. & DAUGHERTY C. H. 2009 — Origin, Diversification and Systematics of the New Zealand Skink Fauna (Reptilia: Scincidae). *Molecular Phylogenetics and Evolution* 52: 470-487.
- CZECHURA G. V. 1981 — The rare scincid lizard, *Nannoscincus graciloides*: a reappraisal. *Journal of Herpetology* 15: 315-320.
- DE QUEIROZ K. 1998 — The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations, in HOWARD D. J. & BERLOCHER S. H. (eds.), *Endless Forms: Species and Speciation*. Oxford University Press, New York: 57-75.
- DRUMMOND A. J. & RAMBAUT A. 2006 — BEAST v1.4. http://beast.bio.ed.ac.uk/Main_Page.
- DRUMMOND A. J., ASHTON B., BUXTON S., CHEUNG M., COOPER A., DURAN C., FIELD M., HELED J., KEARSE M., MARKOWITZ S., MOIR R., STONES-HAVAS S., STURROCK S., THIERER T. & WILSON A. 2011 — Geneious v5.4, available from <http://www.geneious.com/>
- ENNEN J. R., KREISER B. R., QUALLS C. P. & LOVICH J. E. 2010 — Morphological and molecular reassessment of *Graptemys oculifera* and *Graptemys flavimaculata* (Testudines: Emydidae). *Journal of Herpetology* 44: 544-554.
- FELSENSTEIN J. 1985 — Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783-791.
- GREER A. E. 1974 — The generic relationships of the scincid lizard genus *Leiopisma* and its relatives. *Australian Journal of Zoology*, Supplementary Series 31: 1-67.
- GÜNTHER A. 1872 — On some new species of reptiles and fishes collected by J. Brenchley, Esq. *Annals and Magazine of Natural History* (4th series) 10: 421.
- JAFFRÉ T., BOUCHET P. & VEILLON J.-M. 1998 — Threatened plants of New Caledonia: Is the system of protected areas adequate? *Biodiversity and Conservation* 7: 109-135.
- HONDA M., OTA H., KOBAYASHI M., NABHITABHATA J., YONG, H.-S. & HIKIDA, T. 2000 — Phylogenetic relationships, character evolution, and biogeography of the subfamily Lygosominae (Reptilia: Scincidae) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 15: 452-461.
- HONDA M., OTA H., KÖHLER G., INEICH I., CHIRIO L., CHEN S.-L. & HIKIDA T. 2003 — Phylogeny of the lizard subfamily Lygosominae (Reptilia: Scincidae), with special reference to the origin of the New World taxa. *Genes and Genetic Systems* 78: 71-80.
- HUELSENBECK J. & RONQUIST F. 2001 — MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754-755.
- HUTCHINSON M. N., DONNELLAN S. C., BAVERSTOCK P. R., KRIEG M., SIMMS S. & BURGIN S. 1990 — Immunological relationships and generic revision of the Australian lizards assigned to the genus *Leiopisma* (Scincidae: Lygosominae). *Australian Journal of Zoology* 38: 535-554.
- LOVERIDGE A. 1941 — An undescribed skink (*Lygosoma*) from New Caledonia. *Proceedings of the Biological Society of Washington* 54: 193-194.
- MACEY J. J., LARSON A., ANANJEV N. B., FAN Z. & PAPENFUSS T. J. 1997 — Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution* 14: 91-104.
- MADDISON D. R. & MADDISON W. P. 2005 — MacClade: Analysis of Phylogeny and Character Evolution. v4.08. Sinauer Associates, Sunderland, Massachusetts.
- MAYDEN R. L. 1997 — A hierarchy of species concepts: the denouement in the saga of the species problem in CLARIDGE M. F., DAWAH H. A. & WILSON M. R. (eds.), *Species: The Units of Biodiversity*. Chapman and Hall, New York: 381-424.
- NYLANDER J. A. A., WILGENBUSCH J. C., WARREN D. L. & SWOFFORD D. L. 2008 — AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics* 24:581-583.
- PINTAUD J.-C., JAFFRÉ T. & PUIG H. 2001 — Chorology of New Caledonian palms and possible evidence of Pleistocene rain forest refugia. *Comptes Rendus de l'Académie des Sciences Paris, Sciences de la vie / Life Sciences* 324: 453-463.
- POSADA D. & CRANDALL K. A. 1998 — Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817-818.
- RONQUIST F. & HUELSENBECK J. P. 2003 — MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572-1574.
- SADLER R. A. 1986 — A review of the scincid lizards of New Caledonia. *Records of the Australian Museum* 39 (1): 1-66.
- SADLER R. A. 1990 — The scincid lizard genus *Nannoscincus* Günther: a revaluation. *Memoirs of the Queensland Museum* 29 (2): 487-494.
- SADLER R. A. 2010 — Systematic studies of the scincid lizards of New Caledonia. PhD. Thesis, Griffith University, Queensland. 199 p.
- SADLER R. A. & BAUER A. M. 1999 — The scincid lizard genus *Sigaloseps* (Reptilia: Scincidae) from New Caledonia in the southwest Pacific: description of a new species and review of the biology, distribution, and morphology of *Sigaloseps deplanchei* (Bavay). *Records of the Australian Museum* 51: 83-91.
- SADLER R. A. & BAUER A. M. 2000 — The scincid lizard genus *Marmorosphax* (Reptilia: Scincidae) from New Caledonia in the Southwest Pacific: Description of a new species restricted to high-altitude forest in Province Sud. *Pacific Science* 54: 56-62.
- SADLER R. A., BAUER A. M. & SMITH S. A. 2006 — A new species of *Nannoscincus* Günther (Squamata: Scincidae) from high elevation forest in southern New Caledonia. *Records of the Australian Museum* 58: 29-36.
- SADLER R. A., BAUER A. M. & WHITAKER A. H. 2002 — The scincid lizard genus *Nannoscincus* Günther from New Caledonia in the southwest Pacific: a review of the morphology and distribution of species in the

- Nannoscincus mariei* species group, including the description of three new species from Province Nord, in NAJT J. & GRANDCOLAS P. (eds), *Zoologia Neocaledonica* 5, *Mémoires du Muséum national d'Histoire naturelle*, Paris, 187: 233-255.
- SADLIER R. A., BAUER A. M., WHITAKER A. H. & SMITH S. A. 2004 — Two new species of scincid lizards (Squamata) from the Massif de Kopéto, New Caledonia. *Proceedings of the California Academy of Sciences* 55: 208-221.
- SADLIER R. A., SMITH S. A., BAUER A. M. & WHITAKER A. H. 2009 — Three new species of skink in the genus *Marmorosphax* Sadlier (Squamata: Scincidae) from New Caledonia, in GRANDCOLAS P. (ed.), *Zoologia Neocaledonica* 7. Biodiversity studies in New Caledonia. *Mémoires du Muséum national d'Histoire naturelle*, Paris, 198: 373-390.
- SITES J. W. & MARSHALL J. C. 2003 — Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology and Evolution* 18: 464-470.
- SITES J. W. & MARSHALL J. C. 2004 — Operational criteria for delimiting species. *Annual Reviews of Ecology, and Systematics* 35: 199-227.
- SMITH S. A., SADLIER R. A., BAUER A. M., AUSTIN C. C. & JACKMAN T. 2007 — Molecular phylogeny of the scincid lizards of New Caledonia and adjacent areas: Evidence for a Single Origin of the endemic skinks of Tasmantis. *Molecular Phylogenetics and Evolution* 43: 1151-1166.
- STAMATAKIS A., HOOVER P. & ROUGEMONT J. 2008 — A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* 57: 758-771.
- SWOFFORD D. L. 2002 — PAUP: Phylogenetic Analysis Using Parsimony (and Other Methods) Version 4.0. Sinauer Associates, Sunderland, Massachusetts.
- WIENS J. J. & PENKROT T. A. 2002 — Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). *Systematic Biology* 51: 69-91.

APPENDIX 1

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

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

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

Bocourt's terrific skink, *Phoboscincus bocourti* (Brocchi, 1876), and the monophyly of the genus *Phoboscincus* Greer, 1974

Ivan Ineich ⁽¹⁾, Ross A. Sadlier ⁽²⁾, Aaron M. Bauer ^(3*), Todd R. Jackman ⁽³⁾ & Sarah A. Smith ^(3, 4)

⁽¹⁾ Muséum national d'Histoire naturelle, Institut de Systématique, Évolution, Biodiversité, ISYEB - UMR 7205 CNRS, UPMC, EPHE, CP 50, 45, rue Buffon, 75005 Paris, France

⁽²⁾ Section of Herpetology, Australian Museum, 6 College Street, Sydney 2010, NSW, Australia

⁽³⁾ Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA

⁽⁴⁾ Present address: Eco Logical Australia Pty Ltd., 16/56 Marina Boulevard Cullen Bay 0820, NT, Australia

*Corresponding author: aaron.bauer@villanova.edu

ABSTRACT

We use 1344 bp of mitochondrial (ND2) and nuclear (RAG1) DNA sequence data to elucidate the phylogenetic position of the giant New Caledonian scincid lizard *Phoboscincus bocourti* (Brocchi) which has recently been rediscovered after more than a century. This is one of the largest skinks in the world and one of the only New Caledonian skinks for which molecular data are lacking. The species is a member of the monophyletic Tasmantis clade of *Eugongylus* group skinks, which is weakly-supported in this study but is consistent with previous molecular studies of this group. The Tasmantis clade includes the endemic skink genera occurring on New Caledonia, New Zealand and Lord Howe Island. Within this radiation *P. bocourti* receives strong Bayesian support as the sister to its congener, *Phoboscincus garnieri* (Bavay). We were not able to confirm or refute a possible sister relationship between *bocourti* and the extinct giant Tongan skink *Tachygylis microlepis* (Duméril & Bibron) as suggested recently by Ineich on morphological criteria. However, if *P. bocourti* and *T. microlepis* are indeed closest relatives our results would imply that *Tachygylis* is derived from within a New Caledonian clade of skinks.

RÉSUMÉ

Le terrifiant scinque de Bocourt, *Phoboscincus bocourti* (Brocchi, 1876), et la monophylie du genre *Phoboscincus* Greer, 1974.

Nous utilisons 1344 bp de séquences d'ADN mitochondrial (ND2) et nucléaires (RAG1) pour élucider la position phylogénétique du lézard scincidae géant néo-calédonien *Phoboscincus bocourti* (Brocchi) qui a été récemment redécouvert après plus d'un siècle. Il s'agit d'un des plus grands scinques dans le monde et l'un des seuls scinques endémiques néo-calédoniens pour lesquels des données moléculaires font défaut. L'espèce est un membre du clade monophylétique Tasmantis des scinques du groupe *Eugongylus*, qui est faiblement soutenu dans cette étude, mais est compatible avec des études moléculaires antérieures de ce groupe. Le clade Tasmantis comprend les genres de scinques endémiques qui se trouvent en Nouvelle-Calédonie, Nouvelle-Zélande et l'île Lord Howe. Dans cette radiation, *P. bocourti* montre un fort soutien bayésien comme espèce soeur de son congénère, *Phoboscincus garnieri* (Bavay). Nous n'avons pas été en mesure de confirmer ou d'infirmer une relation de proche parenté entre *P. bocourti* et le scinque géant des Tonga disparu *Tachygyia microlepis* (Duméril & Bibron) comme l'a suggéré récemment Ineich sur des critères morphologiques. Toutefois, si *P. bocourti* et *T. microlepis* sont en effet proches, nos résultats impliqueraient que *Tachygyia* soit dérivée d'un clade de scinques néo-calédoniens.

INTRODUCTION

The distinctiveness of the New Caledonian biota has long been recognized and it is considered one of the major global biodiversity hotspots (Myers 1988, 1990; Mittermeier *et al.* 1996; Lowry 1998; Myers *et al.* 2000; Lowry *et al.* 2004). Best known for its botanical uniqueness (Virot 1956; Morat 1993; Morat *et al.* 1986; Jaffré *et al.* 1998), the fauna of New Caledonia is also extremely diverse and largely endemic (Holloway 1979; Chazeau 1993; Platnick 1993; Séret 1997; Haase & Bouchet 1998). Although native amphibians and non-volant mammals are lacking, both marine and terrestrial reptiles, primarily lizards in the families Scincidae and Diplodactylidae, are well represented (Bauer 1989, 1999; Bauer & Sadlier 2000) with nearly a hundred known species.

Perhaps the most enigmatic member of the New Caledonian lizard fauna is *Phoboscincus bocourti*. It is a giant skink (280+ mm SVL) with an elongate body, muscular tail, wide snout, and elongate, curved teeth that inspired its generic name (Greer 1974). The holotype specimen (MNHN 3029) was collected around 1870 by the botanist Benjamin Balansa and described by Brocchi (1876), with the type locality "Nouvelle-Calédonie." Ineich (2009) confirmed that no more specific collection data exist for the specimen and for more than 125 years the source and habitat, and even the continued survival, of *P. bocourti* have been points of conjecture (Börner 1980; Sadlier 1986; Bauer & Vindum 1990; Bauer & Sadlier 2000). The species was rediscovered by Ineich in 2003, collected again in 2005 (Ineich 2006, 2009) and observed again in January 2012 (Ineich & Holden unpubl.), all times on the same small islet off the coast of the Île des Pins, south of the Grande Terre. Ineich (2009) also demonstrated that a large juvenile skink from Îlot Brosse illustrated by Bauer & Sadlier (2000) was referable to *P. bocourti*, rather than *P. garnieri* as these authors had supposed. These southern islands were not visited by Balansa (Ineich 2009), suggesting that the species may once have been (or still is) more widespread, including mainland New Caledonian populations. The history of this species has been discussed in further detail by Ineich (2009).

The species has had a checkered taxonomic history, due largely to its uniqueness in body form, dentition and scalation which has not allowed for a ready association with any other known species of skink. Described by Brocchi in 1876 as *Eumeces bocourti*, it next appeared as a synonym of *Lygosoma garnieri* Bavay — a large endemic New Caledonian skink with a broad distribution on both the Grande Terre and offshore islands (Sadlier 1986; Bauer & Sadlier 2000) — in the catalogue of Lizards in the British Museum of Natural History (Boulenger 1887), and then was recognised as a valid species by Roux (1913) as *Lygosoma bocourti* in a comprehensive monograph of the region's reptile fauna. In the 70 years following Roux's monograph the species was not recognised in either of the classifications of skinks by Smith (1937) or Mittleman (1952), both of whom listed *garnieri* (presumably following the synonymy of Boulenger 1887) but in each instance placing it in a different genus, *Riopa* (*Eugongylus*) and *Tachygyia*, respectively. Both *Eugongylus* and *Tachygyia* are large-bodied lygosomine skinks; the former today represented by five recognized species occurring from Indonesia to the Solomon Islands and the latter monotypic and restricted to Tonga, where it is believed to be extinct (Ineich & Zug 1996; Zug *et al.* 2012).

**FIGURE 1**

New Caledonian giant skinks (A) *Phoboscincus bocourti* from southern offshore islet (identity not provided for conservation security, see Ineich 2009). (B) *P. garnieri* from Plaine des Lacs, Province Sud.

In modern times *bocourti* was first recognised as a valid species when resurrected by Greer (1974) as the type species of his new genus, *Phoboscincus*, in which he also included *garnieri*. The generic distinctiveness of these taxa was contested by Böhme (1976) who placed *Phoboscincus* (and *Tachygylia*) in an expanded *Eugongylus*. Sadlier (1986), in a treatise on the New Caledonian skinks, rejected Böhme's conclusions and resurrected *Phoboscincus*. The monophyly of *Phoboscincus* has since been accepted by most subsequent authors, although Ineich (2009) has suggested that *P. bocourti* may be more closely related to *Tachygylia microlepis* than to *P. garnieri* (see Discussion).

Phoboscincus and most other New Caledonian skinks, as well as *Tachygylia* and *Eugongylus* are all members of a large, purportedly monophyletic group of Australian region skinks recognized by Greer (1979) as the *Eugongylus* group (Hedges & Conn 2012) recently resurrected the family-level name Eugongylidae Welch, 1982 for the members of the *Eugongylus* group, which they regard as part of a more inclusive Lygosomoidea, but we herein retain the earlier usage. While recent morphological (Greer 1989, 1990; Hutchinson 1993; Hutchinson & Donnellan 1993) and molecular studies (Hutchinson *et al.* 1990; Honda *et al.* 2000, 2003; Smith 2001; Whiting *et al.* 2003; Austin & Arnold 2006) have since strongly supported the monophyly of the *Eugongylus* group as an essentially Australasian radiation, there have been few references to the affinities of the New Caledonian skink fauna within this group. Smith *et al.* (2007) used a molecular phylogenetic approach to comprehensively assess the relationships of the New Caledonian skinks, and found support for a monophyletic *Eugongylus* group and within this group for a "Tasmantis" clade that included the endemic skink genera of New Caledonia (exclusive

of the widespread genera *Emoia* and *Cryptoblepharus*), New Zealand, and Lord Howe Island. Their analysis included two specimens of *P. garnieri* which were nested well within the New Caledonian radiation. Smith *et al.* (2007), however, lacked material of *P. bocourti* and, as such, monophyly of the genus has been open to question, particularly in light of alternative hypotheses linking the species to *Tachygia* (Ineich 2009) or *Tachygia* and *Eugongylus* (Böhme 1976). Field observations by Ineich (2009) on recently discovered specimens of *P. bocourti* have provided some insight into the animal's biology, and additional information regarding life coloration and scalation. Of particular significance has been the acquisition of genetic material which now allows us to investigate the relationships of this large, and apparently highly restricted skink and to test the monophyly of *Phoboscincus*.

MATERIALS AND METHODS

Sequences were obtained for the mitochondrial NADH dehydrogenase subunit 2 (ND2; 514 bp); and nuclear recombination activating gene 1 (RAG1; 830 bp) from representatives of all recognized genera of New Caledonian scincid lizards except *Geoscincus*, for which no tissues and no specimens other than the types exist. A total of 42 New Caledonian species from endemic New Caledonian genera and the two *Emoia* spp. occurring on the Loyalty Islands (but not on the Grande Terre) were sampled, as were other representative taxa of lygosomine skinks from Australia, New Guinea, New Zealand, and Lord Howe Island. This includes *Eugongylus rufescens* and *Eugongylus albofasciatus*, which have been proposed by some authors to be closely related to *Phoboscincus*. No samples of *Tachygia microlepis*, which is only known from two type specimens collected in the 19th century on Tongatapu Island (Ineich & Zug 1996; Zug *et al.* 2012), were available for genetic comparisons. Most samples were previously analyzed by Smith *et al.* (2007) and their paper may be consulted for relevant locality and GenBank accession data. Newly added to the data set are two additional *Phoboscincus garnieri* and one *P. bocourti*, two *Eugongylus albofasciatus*, and six additional *Lioscincus nigrofasciolatus* (weakly supported by Smith *et al.* 2007 as the sister taxon of *Phoboscincus garnieri*). For 15 additional species included in Smith *et al.* (2007) new sequences were obtained (KF GenBank accession numbers in Table 1).

DNA was extracted from liver tissue that had been frozen or stored in 95% ethanol using the DNeasy kit (Qiagen). PCR was conducted using Eppendorf mastertaq. ND2 was amplified and sequenced using primers L4437b (Macey *et al.* 1997) and ND2r102 (Sadler *et al.* 2004). RAG1 primers were R13 from Groth and Barrowclough (1999) and an additional reverse primer G425 (primer sequence – 5'- AAA GCA AGG ATA GCG ACA AGA G -3'; Smith 2001; Smith *et al.* 2007). Amplification conditions were: initial denaturation at 94 °C for 2 min, denaturation at 94 °C for 45s, annealing at 52 °C for 45s, and extension at 72 °C for 1 min, for 34 cycles. Negative controls were run for all amplifications. Amplified products were purified using GFX PCR purification columns (Amersham Biosciences). Both strands of each PCR product were purified and sequenced using an ABI 373XL or 3700 automated sequencer. GenBank accession numbers, are provided in Table 1. Alignment of sequences was performed using Clustal X.1.81 (Thompson *et al.* 1997) with default parameters with adjustments by eye using Se-Al v1.0 (Rambaut 1995).

Data were analyzed using maximum parsimony (MP), maximum likelihood (ML) and Bayesian Inference (BI) methods implemented in PAUP* 4.0b10 (Swofford 2002), GARLI version 0.96b8 (Zwickl 2006), and MrBayes version 3.1.2 (Ronquist & Huelsenbeck 2003), respectively. Using hierarchical likelihood-ratio tests (implemented in MrModeltest version 2.0; Nylander 2004) we found the best overall modeling and partitioning strategy for the combined molecular data uses the GTR+I+G model for each codon position in ND2, and HKY+G for each codon position in RAG1. We ran four replicate searches with 5.0 x 10⁶ generations each, sampling every 1,000 generations. Each Bayesian analysis used four chains and default priors. Standard deviations of split frequencies and plots of log-likelihoods over time were examined for stationarity. All analyses appeared to reach stationarity before 1.0 x 10⁶ generations, so the first 1000 trees were discarded as burn-in.

We compared the alternative phylogenetic hypotheses to the optimal ML tree by first generating alternatives using constraint trees in GARLI, then using the Shimodaira-Hasegawa test (SH test) implemented in PAUP* with the GTR+I+G model. The tests were one-tailed using RELL bootstrap with 10,000 bootstrap replicates.

TABLE 1

Specimens used in this study and associated GenBank accession numbers. Additional specimens shown in Figure 2 were previously sequenced by Smith *et al.* (2007), which may be consulted for further details. Numbers following species names correspond to those on Figure 2. Specimens with KF series GenBank numbers were sequenced for this study, others were added from Chapple (2008). In the case of the species most closely related to *Phoboscincus bocourti*, *P. garnieri* and *Lioscincus nigrofasciolatus*, all specimens, including those from Smith *et al.* (2007) — indicated by a single asterisk (*) — are listed. ABTC = Australian Biological Tissue Collection (south Australian Museum, Adelaide), AMS = Australian Museum, Sydney, MNHN = Muséum national d'Histoire naturelle, Paris, NC = New Caledonia, PNG = Papua New Guinea. The specimen of *Phoboscincus bocourti* sequenced in this study was released but Figure 1A serves as a photo voucher.

Specimen (see Figure 2)	Reg. Number	Locality	GenBank ND2	Accession RAG1
<i>Caledoniscincus aquilonius</i>	AMS R163315	NC, Rivière Néhoué	KF130789	KF130814
<i>Caledoniscincus austrocaledonicus</i>	AMS R161115	NC, Mt. Koniambo	KF130790	KF130815
<i>Caledoniscincus festivus</i>	AMS R161881	NC, Monts Kwa Ne Mwa	KF130791	KF130816
<i>Caledoniscincus haplorhinus</i>	AMS R163304	NC, Vallée Phaaye	KF130792	KF130817
<i>Caledoniscincus orestes</i>	AMS R149983	NC, Mt. Panié	JQ743856***	KF130818
<i>Caledoniscincus renevieri</i>	NR 2899	NC, Mt. Aoupinié	KF130793	KF130819
<i>Celatiscincus similis</i>	AMS R13505	NC, Ouaco	KF130794	KF130820
<i>Eugongylus albofasciatus</i> 1	ABTC 98502	PNG, Milne Bay Prov., Misima Id., North Dump Rainforet	KF130787	KF130812
<i>Eugongylus albofasciatus</i> 2	ABTC 98524	PNG, Milne Bay Prov., Misima Id., Lagua Camp	KF130788	KF130813
<i>Graciliscincus shonae</i>	AMS R146508	NC, Mt. Kogis	KF130795	KF130822
<i>Lacertoides pardalis</i>	AMS R158050	NC, Kwa Néie	KF130796	KF130823
<i>Leiolopisma telfarii</i>	no number	Round Island, Mauritius	DQ675259*	KF130811
<i>Lioscincus nigrofasciolatus</i> 1	AMS R163383	NC, Loyalty Islands, Lifou	KF130797	KF130824
<i>Lioscincus nigrofasciolatus</i> 2	AMS R161055	NC, Îles Belep, Île Art	KF130798	KF130825
<i>Lioscincus nigrofasciolatus</i> 3	AMS R161134	NC, Mt. Koniambo	KF130799	KF130826
<i>Lioscincus nigrofasciolatus</i> 4	AMS R138596	NC, Île des Pins	KF130800	KF130827
<i>Lioscincus nigrofasciolatus</i> 5	AMS R147857	NC, Sarraméa	KF130801	KF130828
<i>Lioscincus nigrofasciolatus</i> 6*	AMS R149334	NC, Mt. Panié	DQ675215	DQ675295
<i>Lioscincus nigrofasciolatus</i> 7	AMS R144360	NC, Mt. Dore	KF130802	KF130829
<i>Lioscincus tillieri</i>	AMS R147909	NC, Rivière Bleue	KF130803	KF130830
<i>Marmorosphax kaala</i>	AMS R161091	NC, Mt. Kaala	KF130804	KF130831
<i>Nannoscincus hanchisteus</i>	AMS R149356	NC, Pindai	KF130805	KF130832
<i>Oligosoma alani</i>	FT147	NZ	EF567167**	KF130821
<i>Phoboscincus bocourti</i>	(not collected)	NC, vic. Île des Pins	KF130806	KF130833
<i>Phoboscincus garnieri</i> 1*	AMS R146293	NC, Île des Pins	DQ675236	DQ675316
<i>Phoboscincus garnieri</i> 2	AMS R150065	NC, Tchamba	KF130807	KF130834
<i>Phoboscincus garnieri</i> 3*	AMS R151965	NC, Mt. Dore	DQ675237	DQ675317
<i>Phoboscincus garnieri</i> 4	AMS R151965	NC, Mt. Koghis	KF130808	KF130835
<i>Sigaloseps deplanchei</i>	AMS R147953	NC, Rivière Bleue	KF130809	KF130836
<i>Tropidoscincus boreus</i>	AMS R163185	NC, Boulinda	DQ675241	DQ675321

RESULTS

Analyses of ND2 and RAG1 combined included a total of 1344 nucleotides, of which 663 were variable and 435 were parsimony informative. As reported by Smith *et al.* (2007) analyzing genes separately did not reveal any strongly supported incongruence so we discuss the results of analysis of the two genes combined.

Predictably, given our use of much of the same data, our results (Figure 2) are similar to those of Smith *et al.* (2007). There was weak support (BI posterior probability of 0.91) for a Tasmantis clade of New Caledonian, New Zealand and Lord Howe/Norfolk Island taxa, but virtually no support for relationships among the genera. However, other than *Lioscincus*, which has long been known to be polyphyletic (Sadler & Bauer, 2000; Bauer & Sadler 2000; Sadler *et al.* 2004; Sadler *et al.* 2006), there is generally good support (BI pP 1.0; ML bootstraps >92%; MP bootstraps >91%) for the monophyly of the individual New Caledonian genera, except for *Nannoscincus* for which bootstrap values are somewhat lower. Our data provide strong Bayesian support to support the monophyly of a *Phoboscincus* that includes both *bocourti* and *garnieri*, although there is no support under likelihood and parsimony (BI pP 1.00, ML bootstrap 54%). The SH test rejects *P. bocourti* as the sister to *Eugongylus rufescens* + *E. albofasciatus* (best tree -lnL 16895.39563, -lnL difference of 32.86546 from best tree; $P = 0.043$), which are outside of the Tasmantis clade.

DISCUSSION

Recognition of *Phoboscincus* by Greer (1974) was based on a suite of morphological attributes shared by *P. bocourti* and *P. garnieri*, the combination of which was unique within the *Eugongylus* group of skinks. These included: large size, fused frontoparietal scales and sharply pointed, recurved fang-like teeth in the anterior part of the jaws. Greer (1974) also recognised the other giant Pacific region skink, *Eumeces microlepis* from Tonga, as warranting its own genus diagnosed by virtue of a suite of mainly primitive character states that included large size, fused frontoparietal scales and peg-like teeth, and allocated it to the monotypic *Tachygyia* Duméril & Bibron.

Smith *et al.* (2007) identified a group consisting of ('*Lioscincus*' *nigrofasciolatus* (*Phoboscincus garnieri* + *Lacertoides pardalis*)) with high Bayesian support values but less than 50% bootstrap support. However, several key New Caledonian taxa including '*Lioscincus*' *greeri* (the sister species to *nigrofasciolatus*) and *Phoboscincus bocourti* were not available for that study, nor was *Tachygyia microlepis*. As such, the affinities of these missing taxa has rested on morphological evidence alone.

Ineich (2009) has since provided comparative morphological data identifying significant differences between *garnieri* and *bocourti* with respect to a number of key character states (condition of the lower eyelid, gular plate contact, presence of a pineal light spot, and scale size as expressed by the number of midbody scale rows), concluding *garnieri* was more closely allied to '*Lioscincus*' *nigrofasciolatus* as part of a broader New Caledonian endemic clade, whereas the affinities of *bocourti* lie elsewhere in the Pacific, specifically with *T. microlepis*. Ineich (2009) also identified morphological and probable ecological similarities between *bocourti* and *microlepis* as evidence of relationship between these two taxa, the most significant of these being the presence of a depression in the interparietal, but no corresponding pale parietal spot. These data were considered strong evidence in favour of a common origin for *bocourti* and *microlepis*, rather than similarity through convergence.

FIGURE 2

Phylogeny based on combined, partitioned Bayesian analysis of a 514 bp fragment of the ND2 mitochondrial gene and 830 bp fragment of the RAG1 nuclear gene. Topology and branch lengths taken from the posterior distribution of trees with the highest likelihood value. Support values are shown in the form: Bayesian posterior probability/ML bootstrap support/MP bootstrap support. Support values are not shown for outgroup relationships which receive Bayesian posterior probabilities of less than 0.50. Support values for intraspecific relationships in *Phoboscincus garnieri* and *Lioscincus nigrofasciolatus* not shown.



Sadler (2010) independently assessed morphological characters extensively across the New Caledonian endemic skink genera and across genera within the *Eugongylus* group of skinks to identify concordant morphological apomorphies supporting the genera and suprageneric groupings retrieved in the molecular phylogeny of Smith *et al.* (2007). Apomorphies to support the full complement of taxa in the group ('*Lioscincus*' *nigrofasciolatus* (*Phoboscincus garnieri* + *Lacertoides pardalis*)) as derived by Smith *et al.* are limited to an elevated number of upper labial scales (8 or more) and division of the basal dorsal toe scales (Sadler 2010). Neither is particularly compelling; division of the basal dorsal toe scales appears to have evolved independently in several groups of endemic New Caledonian skinks and an elevated number of upper labial scales is also seen in some larger New Zealand taxa and in *Eugongylus* and is more likely associated with a trend towards fragmentation of head shields with increasing size. There was considerably more morphological evidence to support a close relationship between '*Lioscincus*' *nigrofasciolatus* and *Phoboscincus garnieri* exclusive of *Lacertoides* as suggested by Ineich (2009). Both species share a more extensive suite of apomorphies that includes separation of the chinshields from the lower labial scales by 1-2 rows of small intervening scales (variably in '*Lioscincus*' *nigrofasciolatus* and 3rd chinshield only in *P. garnieri*) and division of the last upper labial obliquely, characters also shared by *Phoboscincus bocourti*. By comparison the apomorphies shared by *Lacertoides* with *Phoboscincus* to the exclusion of '*Lioscincus*' *nigrofasciolatus* (fusion of the frontoparietals), or by *Lacertoides* and '*Lioscincus*' *nigrofasciolatus* to the exclusion of *Phoboscincus* (smooth body scales) are not compelling indicators of relationship and appear to also have evolved numerous times within the *Eugongylus* group.

Our most recent molecular phylogenetic analyses (Figure 2), which now incorporate *Phoboscincus bocourti*, place it as the sister taxon to *Phoboscincus garnieri* and these taxa as sister to '*Lioscincus*' *nigrofasciolatus*, although with weak support in the latter case. We are confidently able to reject Böhme's (1976) hypothesis that *Phoboscincus* is closely allied to *Eugongylus*, however, we were unable to assess scenarios linking *Phoboscincus*, or *P. bocourti* alone, to the extinct *Tachygylus* (Böhme 1976; Ineich 2009). However, if there is a close relationship between *Phoboscincus bocourti* and *Tachygylus* as proposed by Ineich (2009) this would indicate an origin for *Tachygylus* from within the New Caledonian radiation of lygosomines based on the monophyly of *Phoboscincus* as supported by our Bayesian analysis. This is not an unreasonable scenario, given that the New Zealand skink fauna plus the single species occurring on Lord Howe Island and Phillip Island (near Norfolk Island) may be derived from within the New Caledonian lineage (Smith *et al.* 2007; but see Chapple *et al.* 2009) and that the Fijian skink "*Leiopisma*" *alazon*, the relationships of which remain unresolved, is similar in overall appearance to some of the New Zealand *Oligosoma*. Further, as Tonga is an oceanic island group, all of its lizards must have ultimately been derived via overwater dispersal from ancestors presumably further west in the Pacific. Although Tongan endemics studied so far appear to have their closest affinities to Fijian and Samoan taxa (Hamilton 2010; Zug *et al.* 2012), derivation from New Caledonia either directly or indirectly is possible. The probable human-mediated extinction of other large lizards in the Pacific (Zug *et al.* 2012) makes it conceivable that allied taxa may have become extinct on geographically intervening island groups.

The rediscovery of *Phoboscincus bocourti* and the demonstration that it is part of the New Caledonian radiation of lygosomine skinks provide some pieces to the puzzle of this enigmatic lizard. However, its fate on the Grande Terre of New Caledonia (where, based on the travels of its original collector, it must have been first encountered) remains unexplained.

ACKNOWLEDGMENTS

We are indebted to the New Caledonian authorities for their continued support of our herpetological research. In this regard we would particularly like to thank Anne-Claire Goarant (former Chef du service des milieux terrestres) and Cendrine Meresse of the Direction de l'Environnement of the South Province, New Caledonia. Specimen and tissue collect has been made under permit number 6024-3817/DRN/ENV delivered on 28 November 2005 by DENV of Province Sud. We are indebted to David Chapple for providing *Eugongylus* sequence. This research was supported by grants DEB 0108108 and DEB 0515909 from the National Science Foundation to A. M. Bauer and T. Jackman and by a subaward to A. M. Bauer from the BIONEOCAL project (Principal Investigator P. Grandcolas) funded by the Agence Nationale de la Recherche (France).

REFERENCES

- AUSTIN J. J. & ARNOLD E. N. 2006 — Using ancient and recent DNA to explore relationships of extinct and endangered *Leiopisma* skinks (Reptilia: Scincidae) in the Mascarene islands. *Molecular Phylogenetics and Evolution* 39: 503-511.
- BAUER A. M. 1989 — Reptiles and the biogeographic interpretation of New Caledonia. *Tuatara* 30: 39-50.
- BAUER A. M. 1999 — The terrestrial reptiles of New Caledonia: the origin and evolution of a highly endemic herpetofauna, in: OTA, H. (ed.), *Tropical Island Herpetofauna: Origin, Current Diversity, and Conservation*. Elsevier, Amsterdam: 3-25.
- BAUER A. M. & VINDUM J. V. 1990 — A checklist and key to the herpetofauna of New Caledonia, with remarks on biogeography. *Proceedings of the California Academy of Sciences* 47(2): 17-45.
- BAUER A. M. & SADLER R. A. 2000 — The Herpetofauna of New Caledonia. Society for the Study of Amphibians and Reptiles, Ithaca, New York.
- BÖHME W. 1976 — Über die Gattung *Eugongylus* Fitzinger, mit Beschreibung einer neuer Art (Reptilia: Scincidae). *Bonner zoologische Beiträge* 27: 245-251.
- BÖRNER A.-R. 1980 — Über neukaledonische Skinke des *Leiopisma* austrocaledonicum-Komplexes. *Miscellaneous Articles in Saurology* 5: 1-15.
- BOULENGER G. A. 1887 — Catalogue of the Lizards in the British Museum (Natural History), Second Edition. Vol. 3. Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae, Chamaeleonidae. British Museum (Natural History), London.
- BROCCHI P. 1876 — Sur un Scincoidien nouveau appartenant au genre Eumeces. *Bulletin de la Société Philomatique*, Paris série. 6, 13: 95-97.
- CHAPPLE D.G., DAUGHERTY C.H. & RITCHIE P.A. — 2008 Comparative phylogeography reveals pre-decline population structure of New Zealand *Cyclodina* (Reptilia: Scincidae) species. *Biological Journal of the Linnean Society* 95: 388-408.
- CHAPPLE D.G., RITCHIE P.A. & DAUGHERTY C.H. 2009 — Origin, diversification and systematics of the New Zealand skink fauna (Reptilia: Scincidae). *Molecular Phylogenetics and Evolution* 52: 470-487.
- CHAZEAU J. 1993 — Research on New Caledonian terrestrial fauna: achievements and prospects. *Biodiversity Letters* 1: 123-129.
- GREER A. E. 1974 — The generic relationships of the scincid lizard genus *Leiopisma* and its relatives. *Australian Journal of Zoology*, Supplementary Series n° 31: 1-67.
- GREER A. E. 1979 — A phylogenetic subdivision of Australian skinks. *Records of the Australian Museum* 32: 339-371.
- GREER A. E. 1989 — The Biology and Evolution of Australian Lizards. Surrey Beatty and Sons Pty., Ltd., Chipping Norton, NSW.
- GREER A. E. 1990 — Overlap pattern in the preanal scale row: an important systematic character in skinks. *Journal of Herpetology* 24: 328-330.
- GROTH J. G. & BARROWCLOUGH G. F. 1999 — Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. *Molecular Phylogenetics and Evolution* 12: 115-123.
- HAASE M. & BOUCHET P. 1998 — Radiation of crenobiontic gastropods on an ancient continental island: the Hemistomia-clade in New Caledonia (Gastropoda: Hydrobiidae). *Hydrobiologia* 367: 43-129.
- HAMILTON A. M., ZUG G. R. & AUSTIN C. C. 2010 — Biogeographic anomaly or human introduction: A cryptogenic population of tree skink (Reptilia: Squamata) from the Cook Islands, Oceania. *Biological Journal of the Linnean Society* 100: 318-328.
- HEDGES S. B. & CONN C. E. 2012. — A new skink fauna from Caribbean islands (Squamata, Mabuyidae, Mabuyinae). *Zootaxa* 3288: 1-244.
- HONDA M., OTA H., KOBAYASHI M., NABHITABHATA J., YONG H.-S. & HIKIDA T. 2000 — Phylogenetic relationships, character evolution, and biogeography of the subfamily Lygosominae (Reptilia: Scincidae) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 15: 452-461.
- HONDA M., OTA H., KÖHLER G., INEICH I., CHIRIO L., CHEN S.-L. & HIKIDA T. 2003 — Phylogeny of the lizard subfamily Lygosominae (Reptilia: Scincidae), with special reference to the origin of the New World taxa. *Genes and Genetic Systems* 78: 71-80.
- HOLLOWAY J. D. 1979 — A Survey of the Lepidoptera, Biogeography and Ecology of New Caledonia. Dr. W. Junk, The Hague.
- HUTCHINSON M. N. 1993 — Family Scincidae, in: GLASBY C. J., ROSS G. J. B. & BEESLEY P. L. (eds), *Fauna of Australia*, Vol. 2A. Amphibia and Reptilia. Australian Government Printing Service, Canberra: 261-279.
- HUTCHINSON M. N. & DONNELLAN S. C. 1993 — Biogeography and phylogeny of the Squamata, in: GLASBY C. J., ROSS G. J. B., BEESLEY P. L. (eds), *Fauna of Australia*, Vol. 2A. Amphibia and Reptilia. Australian Government Publishing Service, Canberra: 210-220.
- HUTCHINSON M. N., DONNELLAN S. C., BAVERSTOCK P. R., KRIEG M., SIMMS S. & BURGIN S. 1990 — Immunological relationships and generic revision of the Australian lizards assigned to the genus *Leiopisma* (Scincidae: Lygosominae). *Australian Journal of Zoology* 38: 535-554.
- INEICH I. 2004 — Le scinque terrifiant de Bocourt retrouvé en Nouvelle-Calédonie. Press release, Muséum national d'Histoire naturelle, Paris, 3 mars 2004.
- INEICH I. 2006 — Bocourt's terrific skink of New Caledonia is not extinct! *Oryx* 40 (2): 136-136.
- INEICH I. 2009 — Bocourt's Terrific Skink, *Phoboscincus bocourti* (Brocchi, 1876) (Squamata, Scincidae, Lygosominae), in Grandcolas P. (ed.), *Zoologia Neocaledonica* 7. Biodiversity studies in New Caledonia. *Mémoires du Muséum national d'Histoire naturelle*, Paris 198: 149-174.
- INEICH I. & ZUG G. R. 1996 — *Tachygia*, the giant Tongan skink: Extinct or extant? *Cryptozoology* 12: 30-35.
- JAFFRÉ T., BOUCHET P. & VEILLON J.-M. 1998 — Threatened plants of New Caledonia: is the system of protected areas adequate? *Biodiversity and Conservation* 7: 109-135.
- LOWRY P.P. II. 1998 — Diversity, endemism, and extinction in the flora of New Caledonia: a review, in PENG C. I. & LOWRY P. P. II (eds), *Rare, Threatened, and Endangered Floras of Asia and the Pacific Rim*. Institute of Botany, *Academia Sinica Monograph Series* n° 16. Taipei: 181-206.
- LOWRY P.P. II., MUNZINGER J., BOUCHET P., GÉRAUX H., BAUER A. M., LANGRAND O. & MITTERMEIER R. A. 2004 — New Caledonia, in MITTERMEIER, R.A., GIL, P.R., HOFFMANN, M., PILGRIM, J., BROOKS, T., MITTERMEIER, C.G., LAMOREUX, J., DA FONSECA, G.A.B. (eds), *Hotspots Revisited*. CEMEX, Mexico City: 192-197.
- MACEY J. R., LARSON A., ANANJEVA N. B. & PAPENFUSST J. 1997. — Evolutionary shifts in three major structural features of the mitochondrial genome among iguanian lizards. *Journal of Molecular Evolution* 44: 660-674.

- MITTERMEIER R. A., WERNER T. B. & LEES A. 1996 — New Caledonia – a conservation imperative for an ancient land. *Oryx* 30: 104-112.
- MITTLEMAN M. B. 1952 — A generic synopsis of the lizards of the subfamily Lygosominae. *Smithsonian Miscellaneous Collection* 117(17): 1-35.
- MORAT P. 1993 — Our knowledge of the flora of New Caledonia: endemism and diversity in relation to vegetation types and substrates. *Biodiversity Letters* 1: 72-81.
- MORAT P., JAFFRÉ T., VEILLON J.-M. & MACKEE H. S. 1986 — Affinités floristiques et considérations sur l'origine des maquis miniers de la Nouvelle-Calédonie. Bulletin du Muséum national d'Histoire naturelle, Paris, 4e, 8, sect. B, *Adansonia* n° 2, 133-182.
- MYERS N. 1988 — Threatened biotas: "hot spots" in tropical forests. *The Environmentalist* 8: 187-208.
- MYERS N. 1990 — The biodiversity challenge: expand hot-spot analysis. *The Environmentalist* 10: 243-256.
- MYERS N., MITTERMEIER R. A., MITTERMEIER C. G., DA FONSECA G. A. B. & KENT J. 2000 — Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- NYLANDER J. A. 2004 — MrModelTest. 2.0. Distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala.
- PLATNICK N. I. 1993 — The araneomorph spider fauna of New Caledonia. *Biodiversity Letters* 1: 102-106.
- RAMBAUT A. 1995 — Se-Al. Sequence alignment editor. Evolutionary Biology Group, University of Oxford, Oxford.
- RONQUIST F. & HUELSENBECK J. P. 2003 — MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572-1574.
- ROUX J. 1913 — Les reptiles de la Nouvelle-Calédonie et des Îles Loyalty, in SARASIN F. & ROUX J. (eds.), Nova Caledonia, Zoologie, Vol. 1(2). C.W. Kreidels Verlag, Wiesbaden: 79-160.
- SADLIER R. A. 1986 — A review of the scincid lizards of New Caledonia. *Records of the Australian Museum* 39: 1-66.
- SADLIER R. A. 2010 — Systematic studies of the scincid lizards of New Caledonia. PhD. Thesis, Griffith University, Queensland. 199 p.
- SADLIER R. A. & BAUER A. M. 2000 — The scincid lizard genus *Marmorosphax* (Reptilia: Scincidae) from New Caledonia in the Southwest Pacific: Description of a new species restricted to high-altitude forest in Province Sud. *Pacific Science* 54: 56-62.
- SADLIER R. A., BAUER A. M. & SMITH S. A. 2006 — A new species of *Nannoscincus* Günther (Squamata: Scincidae) from high elevation forest in southern New Caledonia. *Records of the Australian Museum* 58: 29-36.
- SADLIER R. A., BAUER A. M., WHITAKER A. H. & SMITH S. A. 2004 — Two new scincid lizards (Squamata: Scincidae) from the Massif de Kopéto, northwestern New Caledonia. *Proceedings of the California Academy of Sciences* 55: 208-221.
- SADLIER R. A., WHITAKER A. H., WOOD P. L., JR. & BAUER A. M. — 2012 A new species of scincid lizard in the genus *Caledoniscincus* (Reptilia: Scincidae) from northwest New Caledonia. *Zootaxa* 3229: 47-57.
- SÉRET B. 1997 — Les poissons d'eau douce de Nouvelle-Calédonie: implications biogéographiques de récentes découvertes. *Mémoires du Muséum national d'Histoire naturelle*, Paris 171: 369-378.
- SMITH M. A. 1937 — A review of the genus *Lygosoma* (Scincidae: Reptilia) and its allies. *Records of the Indian Museum* 39: 213-234.
- SMITH S. A. 2001 — A molecular phylogenetic study of the Eugongylus group of skinks. Ph.D. thesis, University of Adelaide.
- SMITH S. A., SADLIER R. A., BAUER A. M., AUSTIN C. C. & JACKMAN T. 2007 — Molecular phylogeny of the scincid lizards of New Caledonia and adjacent areas: Evidence for a single origin of the endemic skinks of Tasmantis. *Molecular Phylogenetics and Evolution* 43: 1151-1166.
- Swofford D. L. 2002 — PAUP*. Phylogenetic Analysis Using Parsimony (* and other methods). Sinauer Associates, Sunderland, MA.
- THOMPSON J. D., GIBSON T. J., PLEWNIAC F., JEANMOUGIN F. & HIGGINS D. G. 1997 — The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 24: 4876-4882.
- VIROT R. 1956 — La végétation canaque. *Mémoires du Muséum national d'Histoire naturelle*, Paris n.s., B 7: 1-398.
- WHITING A. S., BAUER A. M. & SITES J. W. JR. 2003 — Phylogenetic relationships and limb loss in sub-saharan African scincine lizards (Squamata: Scincidae). *Molecular Phylogenetics and Evolution* 29: 582-598.
- ZUG G. R., INEICH I., PREGILL G. & HAMILTON A. M. 2012 — Lizards of Tonga with description of a new Tongan treeskink (Squamata: Scincidae: *Eomoia samoensis* Group). *Pacific Science* 66: 225-237.
- ZWICKL D. J. 2006 — Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. dissertation, The University of Texas at Austin.

Localized endemism in the southern ultramafic bio-region of New Caledonia as evidenced by the lizards in the genus *Sigaloseps* (Reptilia: Scincidae), with descriptions of four new species

Ross A. Sadlier ⁽¹⁾, Aaron M. Bauer ⁽²⁾, Perry L. Wood, Jr. ^(2,3), Sarah A. Smith ^(2,4)
†Anthony H. Whitaker ⁽⁵⁾, Hervé Jourdan ⁽⁶⁾ & Todd Jackman ⁽²⁾

⁽¹⁾ Section of Herpetology, Australian Museum, 6 College Street, Sydney 2000, NSW, Australia
rosss@austmus.gov.au

⁽²⁾ Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA

⁽³⁾ Department of Biology and Bean Life Science Museum, Brigham Young University Provo, UT, 84602, USA

⁽⁴⁾ Eco Logical Australia Pty Ltd., 16/56 Marina Boulevard Cullen Bay 0820, NT, Australia

⁽⁵⁾ Whitaker Consultants Limited, 270 Thorpe-Orinoco Road, Orinoco, RD1, Motueka 7161, New Zealand

⁽⁶⁾ Institut de Recherche pour le Développement, Laboratoire de Zoologie Appliquée - BPA5 98848 Nouméa Cedex / New Caledonia

ABSTRACT

The scincid genus *Sigaloseps* is reviewed in the light of information derived from new collections made over the past 10 years. The results from field, morphological and genetic studies reveal a complex of three taxa currently masquerading under *Sigaloseps deplanchei*, two taxa under *Sigaloseps ruficauda*, and another species with no obvious morphological affinities to any described taxon. All species are restricted to habitats on ultramafic surfaces of southern New Caledonia. In the genetic analysis three taxa restricted to high-elevation habitats in the southern ranges constitute a well supported group. The speciation within this group most likely reflects contraction of forest to mountain top refugia resulting from changes in climate during the deep and recent history of the genus. Given their extremely small ranges, and the potential for loss or degradation of preferred habitat from fire and invasive species, these three high-elevation lizard species are at a moderate level of threat, and are categorized as Vulnerable when assessed under IUCN criteria. The new species described from the northern edge of the southern ultramafic region is known from only two locations, both of which are threatened,

SADLIER R. A., BAUER A. M., WOOD P. L., SMITH S. A., WHITAKER A. H., JOURDAN H. & JACKMAN T. 2014 — Localized endemism in the southern ultramafic bio-region of New Caledonia as evidenced by the lizards in the genus *Sigaloseps* (Reptilia: Scincidae), with descriptions of four new species, in GUILBERT É., ROBILLARD T., JOURDAN H. & GRANDCOLAS P. (eds), *Zoologia Neocaledonica 8. Biodiversity studies in New Caledonia*. Muséum national d'Histoire naturelle, Paris: 79-113 (Mémoires du Muséum national d'Histoire naturelle; 206). ISBN: 978-2-85653-707-7.

and would be categorized as Endangered. A revised *Sigaloseps deplanchei*, now restricted mainly to the Grande Sud of southern New Caledonia, shows significant, regionally discrete, intraspecific genetic sub-structuring. One or more populations from each subgroup of *Sigaloseps deplanchei* are represented within Provincial reserves, but the majority of the range of each sub-group is likely to be in areas that are currently exploited for nickel mining or lie within areas which are under mining concessions.

RÉSUMÉ

Endémisme dans la bio-région du sud ultramafique de Nouvelle-Calédonie illustrés par les lézards du genre *Sigaloseps* (Reptile : Scincidae), avec la description de quatre nouvelles espèces.

Les scinques du genre *Sigaloseps* sont révisés à la lumière des informations obtenues à partir des collections réalisées ces dix dernières années. Les résultats du terrain, des études morphologiques et de la génétique mettent en évidence un complexe de trois taxons autrefois confondus sous le binôme *Sigaloseps deplanchei*, deux taxons identifiés comme *Sigaloseps ruficauda* et une autre espèce sans affinités morphologiques apparentes avec un autre taxon décrit. Toutes les espèces sont restreintes à des habitats situés sur des substrats ultramafiques du sud de la Nouvelle-Calédonie. Dans notre analyse génétique, trois taxons constituent un groupe bien individualisé limité à des habitats de zones d'altitude dans les massifs du sud. La spéciation à l'intérieur de ce groupe reflète probablement les contractions de la forêt vers des refuges au sommet des montagnes liées aux changements climatiques qui se sont déroulés durant l'histoire ancienne et récente du genre. Leur répartition géographique extrêmement étroite et la vulnérabilité de leurs habitats préférentiels par le feu (perte ou dégradation) et les espèces invasives rendent ces espèces d'altitude menacées et nous amènent à les ranger dans la catégorie 'Vulnérable' selon les critères de l'UICN. La nouvelle espèce décrite de la bordure nord de la région ultramafique du sud est connue seulement de deux localités, toutes deux menacées, et a été rangée dans la catégorie UICN 'En danger'. La forme révisée de *Sigaloseps deplanchei*, à présent restreinte principalement à la Grande Sud du sud de la Nouvelle-Calédonie, présente une sous-structuration génétique intra-spécifique régionale significative mais discrète. Une ou plusieurs populations de chaque sous-groupe de *Sigaloseps deplanchei* sont représentées dans des réserves naturelles provinciales, mais la majorité de la répartition géographique de chaque sous-groupe est vraisemblablement localisée dans des zones qui sont actuellement exploitées pour le nickel ou qui se situent dans des zones sous concession minière.

INTRODUCTION

Ultramafic surfaces cover about 5,500 km² or about a third of the total land area of the main island of New Caledonia or Grande Terre (Jaffré *et al.* 1987). These surfaces are characteristically rich in iron and magnesium, and several heavy metals, most notably nickel, and are (or will be) under considerable pressure from mining activities (Richer de Forges & Pascal 2008; Pascal *et al.* 2008). Recent fieldwork in combination with systematic studies have resulted in the discovery and description of a number of new taxa in the ultramafic ranges of the southern (Sadlier *et al.* 2006a; Bauer *et al.* 2008) and west-central/north-west regions of the island (Sadlier *et al.* 2004a, 2004b, 2006b, 2009; Bauer *et al.* 2006), identifying each area as having a rich and highly endemic lizard fauna.

The distinctiveness of the southern ultramafic region as an area of endemism for lizards has been highlighted in earlier reviews (Bauer & Sadlier 1993, 2000). Ongoing studies have revealed an extensive suite of skinks restricted to this region that includes nine species within four regionally endemic genera (*Sigaloseps* – 6(*3) species; *Graciliscincus* – 1 species; *Simiscincus* – 1 species; *Lacertoides* – 1 species), and a further six regionally restricted species within more widespread genera (*Nannoscincus mariei*; *Nannoscincus fuscus*; *Nannoscincus garrulus*(*); *Marmorosphax montana*(*); *Tropidoscincus variabilis*; *Lioscincus tillieri*), five of which(*) are confined to high-elevation forest habitat on the summits of the ranges. There is also a suite of diplodactylid geckos restricted to the region (Bauer *et al.* 2008 ; 2012). The high number of lizard species restricted to the southern ultramafic ranges identifies this region as of considerable conservation significance for the endemic New Caledonian lizard fauna.

A review of the genus *Sigaloseps* (Sadlier & Bauer 1999) assessed morphological variation in the type species *deplanchei* and described a new species, *S. ruficauda*, from high-elevation habitat on Mt Mou (type locality) and nearby Mt Ouin in the southern ranges of Grande Terre. Recognition of *S. ruficauda* was at the time based on morphological criteria alone,

and its presence on Mt Ouin was represented by a single individual. Subsequently field work in the region resulted in the collection of specimens similar in morphology to *S. ruficauda* from Mt Ouin, and nearby Mt Humboldt and the Massif du Kouakoué. However, investigations using the ND2 mitochondrial DNA gene have identified significant genetic divergence between the type population of *S. ruficauda* from Mt Mou and those on Mt Ouin and Mt Humboldt. Specimens referred to each genetic lineage show no significant differentiation in scalation, but do show concordant differences in both the color pattern of the tail and the intensity of the reddish tail color. Field studies on Mt Humboldt also resulted in the discovery of a morphologically distinctive new species of *Sigaloseps* from high-elevation forest. This taxon is the sister to *S. ruficauda* sensu stricto in the genetic analyses, but with a very low level of genetic differentiation between the two taxa, indicating a recent speciation event.

Further field work in the southern region of Grande Terre in combination with broad-scale genetic studies funded by the BIONEOCAL initiative has provided information that redefines *S. deplanchei*, restricting it in distribution to the Grande Sud and identifying extensive regionally concordant genetic differentiation within the taxon. These studies also recognize a further two taxa that were previously included within *S. deplanchei*. One of the two additional taxa identified has a distribution that includes the central and northern areas of the southern ultramafic region and adjacent east-central region, and is recognized as a distinct species on both morphological and genetic criteria. The other taxon is known only from few sites in the southeast of the region, is very similar in overall appearance to *S. deplanchei*, with modal differences in the scalation associated with the eye providing a level of concordant morphological differentiation between the two lineages. However, some overlap in the distribution of character states prevents them from being completely diagnostic for each putative taxon. For this reason recognition of the new taxon draws support primarily from the genetic data which identifies the two taxa as being highly divergent in their level of genetic difference and in their relationship with each other.

As such, our investigations into *Sigaloseps* has not only identified a complex pattern of narrow-range (altitude dependent) endemism, but also broader scale (altitude independent) localized endemism within the southern ultramafic region, indicating the potential for the evolution of localized endemics in these ranges driven by cladogenic factors other than historical isolation on mountain summits. However, our understanding of the biogeography of southern Grande Terre is complicated by many areas having been not, or only poorly, investigated, particularly the summits of a number of peaks, and the current state of knowledge is likely to represent a significant underestimate of the extent of endemism in the region. As such, the ultramafic ranges of southern New Caledonia, and in particular the high elevation habitats, are here recognized as the areas of great conservation significance for lizards on the Grande Terre, and priority areas for future investigation.

MATERIALS AND METHODS

SYSTEMATICS

Acronyms. Specimen abbreviations are prefixed as follows: AMS - Australian Museum, Sydney; MNHN - Muséum national d'Histoire naturelle, Paris.

Measurements. The following characters were scored for each specimen where possible: snout to vent length - measured from tip of snout to caudal edge of anal scales; axilla to groin distance - measured from middle of base of the forelimb to middle of base of hindlimb; forelimb to snout length - measured from tip of snout to middle of base of forelimb; hindlimb length - measured from middle of base of hindlimb to tip of fourth toe including nail; tail length - measured from caudal edge of anal scales to tip of tail, on complete original tails only. Body measurements are expressed as percentages of snout to vent length (SVL) in the taxon accounts.

Scalation. Head scalation generally follows Sadler (1986). For characters used in Table 1 the abbreviation is given in parentheses: midbody scale rows (MBR) - number of longitudinal scale rows around body counted midway between axilla and groin; dorsal scale rows (DSR) - number of scales in a row from first scale posterior to parietal scale to last scale at the level of vent opening; fourth finger (FFS) and toe (FTS) scales - number of dorsal scales on fourth digit of hand and

foot, distal scale contains claw and basal scale broadly contacts adjacent basal scale of third finger or toe; fourth finger (FFL) and toe (FTL) lamellae - number of ventral scales on fourth digit of hand and foot, distal scale contains claw and basal scale is last largely undivided scale at a point level with intersection of third and fourth digits. Bilaterally scoreable scalation characters were counted on both sides and the mean value used; in the holotype description these values are presented as left/right values.

Phalangeal formulae for the manus and pes and the number of presacral and postsacral vertebrae (complete original tails only) were determined from radiographs prepared using a Eresco AS2 X-ray machine at exposures of 30 sec at 30 kV.

PHYLOGENETIC STUDIES

Character polarities. Follow Sadlier (2010) for morphological characters.

Genetic studies. Molecular Phylogenetics: we obtained sequence data from a 514 bp fragment of the mitochondrial NADH dehydrogenase 2 (ND2) gene from 41 samples from 17 locations determined on morphological criteria as representing the species *Sigaloseps deplanchei*. This sampling included the 4 samples later determined as a separate lineage *Sigaloseps* sp. from Rivière Bleue and Pourina River (2 locations), 13 samples from 3 locations in the north and central regions of the southern ultramafic block already determined on morphological criteria as representing a new species of *Sigaloseps*. It also included two samples representing the species *Sigaloseps ruficauda* from the type locality Mt. Mou, two samples from two high-elevation locations (Mt Ouin and Mt Humboldt) representing individuals similar in morphology *Sigaloseps ruficauda*, and three samples from high elevation at Mt Humboldt determined on morphological criteria as representing a new species of *Sigaloseps* (Appendix 1). Outgroups were selected on the basis of a broader phylogenetic analysis of New Caledonian skinks by Smith *et al.* (2007) and sequences for these were obtained from Genbank (Appendix 1).

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

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

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

The Akaike Information Criterion (AIC) as implemented in ModelTest v3.7 (Posada & Crandall 1998) was used to calculate the best-fit model of evolution for both ML and BI. For both model-based approaches we partitioned our data

set by codon position. The General Time Reversal (GTR) plus (I) for proportional sites plus (G) for gamma distribution among site variation was applied for all codon positions.

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

The Bayesian analysis was carried out in MrBayes v3.1 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) using default priors. The GTR+I+G model was applied to each codon position. Two simultaneous parallel runs were performed with 4 chains per run, 3 hot and 1 cold following default settings. The analysis was run for 10,000,000 generations and sampled every 1000 generations from the Markov Chain Monte Carlo (MCMC). The analysis was halted after 10,000,000 generations if the average standard deviation split frequency was below 0.01. The program Are We There Yet? (AWTY) (Nylander *et al.* 2008) was used to plot the log likelihood scores against the number of generations to assess convergence and to determine the appropriate burn-in. A consensus tree from the two runs was built using TreeAnnotator v1.6.1 (Drummond & Rambaut 2006). Nodes that had posterior probabilities above 0.95 were considered significantly supported. The content and order of authors for the description of each species reflects the individual contributions of those individuals to the discovery and recognition of that species, and as such does not necessarily reflect the content and arrangement of authors for this article as a whole.

RESULTS

All analytical methods resulted in the same tree topology except for several poorly-supported branches within *Sigaloseps deplanchei* sensu stricto and relationships strongly supported by high bootstrap values under maximum likelihood (Figure 1) were also strongly supported by Bayesian and parsimony results (not shown). The results revealed five well supported groups within *Sigaloseps* (Figure 1), each representing a distinct evolutionary lineage:

Group 1: A taxon formerly included within *Sigaloseps deplanchei* sensu lato and represented by populations from the southeast of the southern ultramafic region at Rivière Bleue and Pourina River and here described as *Sigaloseps conditus* n. sp.

Group 2: A taxon formerly included within *Sigaloseps deplanchei* sensu lato and represented by populations in the central (Tontouta valley) and northern (Pic Ningua) areas of the southern ultramafic region, and coastal ultramafic ranges in the east-central region (Nakéty) and here described as *Sigaloseps pisinnus* n. sp.

Group 3: A lineage of three taxa from the interior ranges of the southern ultramafic region: one representing populations on the adjacent peaks of Mt Ouin and Mt Humboldt formerly included under *Sigaloseps ruficauda* and here described as *Sigaloseps ferrugicauda* n. sp.; one representing the type population of *Sigaloseps ruficauda* sensu stricto from Mt Mou; and one representing a taxon from Mt Humboldt that is morphologically very distinct but shows a low level of genetic differentiation from *Sigaloseps ruficauda* and is here described as *Sigaloseps balios* n. sp.

Group 4: a widespread taxon that represents *Sigaloseps deplanchei* sensu stricto and which includes a complex of genetically discreet parapatric sub-populations distributed across ultramafic surfaces of southern Grande Terre.

The genetic data identifies Group 4 as a well supported lineage comprising the majority of samples currently assignable to *Sigaloseps deplanchei* s.s.. Populations within this lineage are diagnosable on morphological criteria from those in Group 2 (*S. pisinnus* n. sp.) and Group 3 (*S. ferrugicauda* n. sp. (*Sigaloseps ruficauda* s.s. + *S. balios* n. sp.)), but not the Group 1 genetic lineage (*S. conditus* n. sp.) from the southeast of the region. As such, recognition of the in Group 1 populations as distinct from Group 4 draws significantly on the high level of genetic differentiation between the two lineages (14.3–18.2%, Table 1), and their placement within the scheme of genetic relationships for the genus in which the populations in Group 4 receive high support as the sister lineage to the Group 3 taxa (species in the *Sigaloseps* ‘*ruficauda*’ group), whereas the taxon represented by Group 1 lies outside this sub-group of taxa.

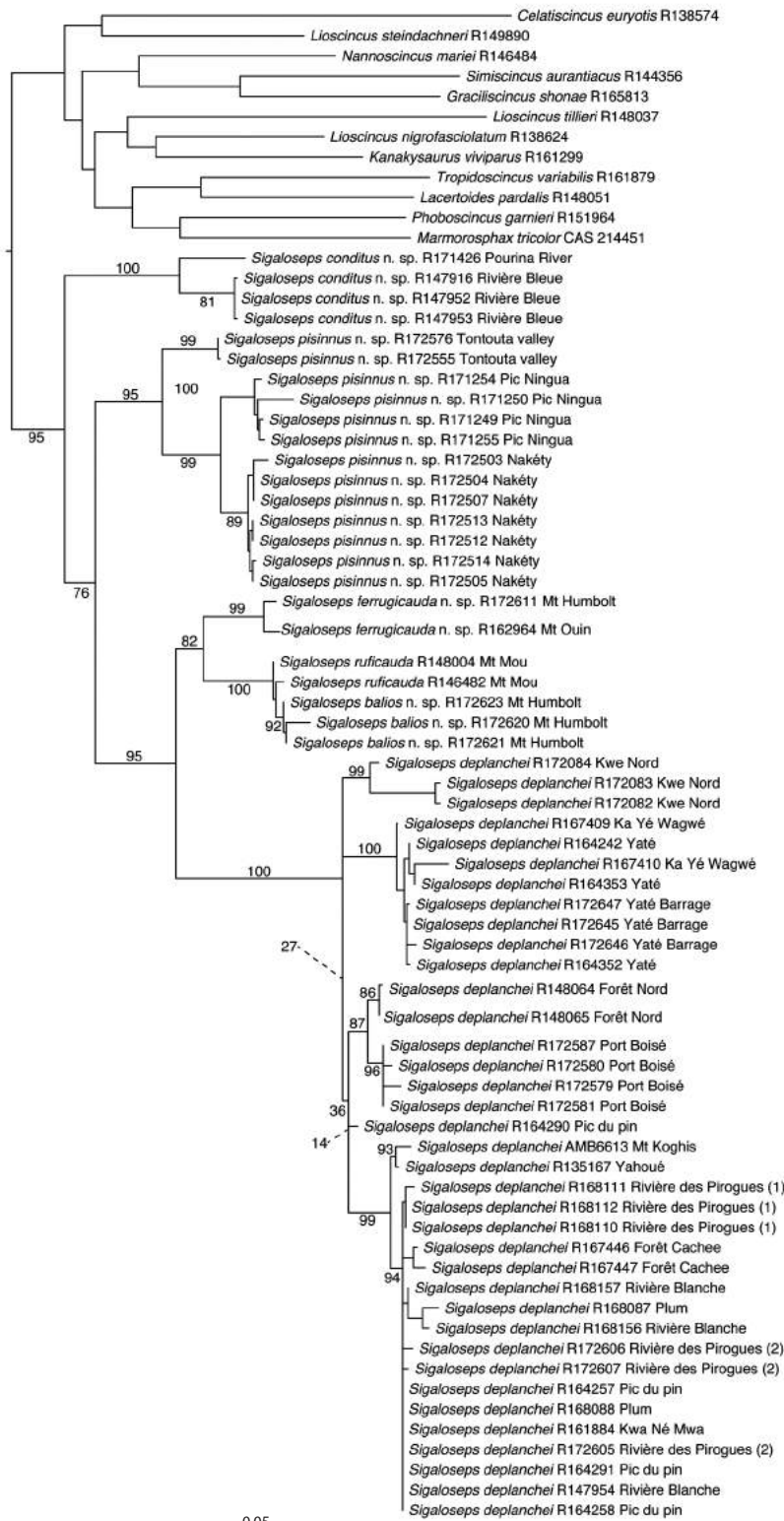


FIGURE 1

Phylogenetic relationships amongst the species and populations of *Sigaloseps*. Maximum Likelihood topology with bootstrap support values. Additional phylogenetic analyses (Maximum parsimony and Bayesian Inference) were conducted and obtained similar nodal support.

TABLE 1

Pairwise matrix of genetic distances (Uncorrected "P") between species of *Sigaloseps* (below the diagonal) and within each species (on diagonal in bold) for the ND2 mitochondrial DNA gene.

	<i>S. deplanchei</i> (Group 4)	<i>S. conditus</i> n.sp. (Group 1)	<i>S. pisinnus</i> n. sp. (Group 2)	<i>S. ruficauda</i> (Group 3)	<i>S. ferrugicauda</i> n. sp. (Group 3)	<i>S. balios</i> n. sp. (Group 3)
1	0.0-9.7 %					
2	14.3-18.2 %	0.3-7.6 %				
3	12.5-19.4 %	13.2-16.1 %	0.7-9.3 %			
4	11.6-16.1 %	14.4-15.6 %	12.6-15.7 %	0.70 %		
5	10.7-15.9 %	15.5-15.8 %	12.0-15.6 %	8.0-9.1 %	0.0-1.9 %	
6	12.2-16.9 %	14.4-16.2 %	12.6-16.0 %	0.9-2.7 %	8.7-9.8 %	0.1-1.9 %

TABLE 2

Differences in body and tail size, and scalation between the species of *Sigaloseps*.

	<i>S. deplanchei</i>	<i>S. conditus</i> n. sp.	<i>S. pisinnus</i> n. sp.	<i>S. ruficauda</i>	<i>S. ferrugicauda</i> n. sp.	<i>S. balios</i> n. sp.
MBR range mean $\pm$ sd	n = 25 26-30 28.0 $\pm$ 0.62	n = 9 26-28 26.2 $\pm$ 0.67	n = 17 22-24 23.9 $\pm$ 0.48	n = 7 26-28 26.6 $\pm$ 0.97	n = 4 26-28 26.5 $\pm$ 1.00	n = 3 26-28 26.7 $\pm$ 1.15
DSR range mean $\pm$ sd	n = 25 49-55 52.4 $\pm$ 1.78	n = 9 48-52 50.2 $\pm$ 1.30	n = 17 48-55 51.6 $\pm$ 2.32	n = 7 53-60 56.6 $\pm$ 2.30	n = 4 53-56 54.5 $\pm$ 1.29	n = 3 58-61 59 $\pm$ 1.70
FFS range mean $\pm$ sd	n = 25 8-9 8.15 $\pm$ 0.30	n = 9 6-8 7.6 $\pm$ 0.60	n = 17 6-9 7.62 $\pm$ 0.65	n = 7 7-9 8.1 $\pm$ 0.75	n = 4 8-9 8.25 $\pm$ 0.50	n = 3 8-9 8.5 $\pm$ 0.50
FFL range mean $\pm$ sd	n = 24 11-14 12.2 $\pm$ 0.93	n = 9 11-14 11.9 $\pm$ 0.80	n = 17 9-11 10.3 $\pm$ 0.73	n = 7 9-15 11.8 $\pm$ 0.80	n = 4 12-13 12.75 $\pm$ 0.50	n = 3 12-14 12.8 $\pm$ 0.76
FTS range mean $\pm$ sd	n = 25 10-12 11.15 $\pm$ 0.41	n = 9 11-12 11.1 $\pm$ 0.33	n = 17 10-12 11.0 $\pm$ 0.41	n = 7 10-13 11.1 $\pm$ 1.10	n = 4 10-12 11.1 $\pm$ 0.63	n = 3 11-12 11.2 $\pm$ 0.29
FTL range mean $\pm$ sd	n = 25 23-29 26.1 $\pm$ 1.48	n = 7 25-29 26.4 $\pm$ 1.28	n = 16 20-25 22.9 $\pm$ 1.37	n = 7 21-28 24.7 $\pm$ 1.95	n = 4 24-28 26.1 $\pm$ 1.38	n = 3 23-25 24.2 $\pm$ 0.76
SVL Maximum mean	n = 25 46 40.3	n = 9 46 42	n = 17 38.5 34.1	n = 3 56 47.3	n = 4 60 56.4	n = 3 50 46.2
TL range mean	n = 9 87.5-110.8 100.8	n = 0	n = 2 128.9-139.5 128.9	n = 1 152.6	n = 0	n = 1 128.4

Populations in Group 2 (*S. pisinnus* n. sp.) from the central and northern regions of the southern ultramafic ranges and coastal ultramafic ranges of the east-central region form a well-supported and highly differentiated genetic lineage (12.5-19.4%), which although superficially similar in appearance the Group 4 taxon to (*S. deplanchei* s.s.) show significant differences in scalation (Table 2) and subtle differences in color pattern, which in combination provides strong support for recognition of this taxon as a distinct species.

The complex of high-elevation populations included in Group 3 form two moderately well-differentiated lineages (8.0-9.1% - Table 1). One lineage includes the population from Mt Mou, the type locality of *Sigaloseps ruficauda* s.s., and a morphologically distinctive taxon from Mt Humboldt (*S. balios* n. sp.). The other lineage contains populations from Mt Ouin and Mt Humboldt (*S. ferrugicauda* n. sp.), the former of these previously being included under *Sigaloseps ruficauda* sensu lato (Sadlier & Bauer 1999). The taxa represented by populations from Mt Mou (*Sigaloseps ruficauda* s.s.) and Mt Ouin and Mt Humboldt (*S. ferrugicauda* n. sp.) share similarities in overall appearance, scalation and color pattern, the main morphological difference between the two being in coloration, most significantly the intensity of the red tail coloration. The third member of this complex (*S. balios* n. sp.) is readily distinguished by features of tail and ventral coloration, and some difference in scalation (Table 2). However, it shows only a low level of differentiation (0.9-2.7%) from its allopatric sister taxon *Sigaloseps ruficauda* s.s., indicating a recent and rapid divergence of these two taxa.

TABLE 3
Pairwise matrix of genetic distances (Uncorrected «P») between major sub-groups of *Sigaloseps deplanchei* (below the diagonal) and within the sub-groups (on diagonal in bold) for the ND2 mitochondrial DNA gene.

	'western' 1	'eastern' 2	'southern' 3	Kwé Nord 4	Pic du Pin 5
1	0-3.2 %				
2	4.6-8.4 %	0.2-3.5 %			
3	3.5-7.2 %	3.1-7.0 %	0-2.9 %		
4	5.3-10.2 %	4.4-11.6 %	2.4-8.3 %	0.7-4.8 %	
5	4.0-5.3 %	4.4-6.4 %	2.6-4.1 %	3.3-7.1 %	0

SYSTEMATIC PART

Family SCINCIDAE Gray, 1825

Genus **SIGALOSEPS** Sadlier, 1986

Type species. *Lygosoma deplanchei* Bavay, 1869.

DIAGNOSIS — [*denotes apomorphic character states within the *Eugongylus* group as defined by Sadlier, (2010)]: The species of *Sigaloseps* are small in size with a maximum snout-vent length of 38.5 mm for *S. pisinnus* n. sp. to 60 mm for *S. ruficauda* s.s., have a stout body, moderately well developed limbs and digits, and a short (~100% of SVL for *S. deplanchei* s.s.) to moderately long tail (150% for *S. ruficauda* s.s.). The ear opening is moderately large and *lacks obviously enlarged lobules around the anterior edge.

Scalation. Body scales smooth; *no distinct supranasal; naris situated within a single undivided nasal scale; frontonasal broader than long; prefrontals moderately large and narrowly to moderately separated; frontal longer than wide; supraoculars four; *frontoparietals fused; interparietal distinct; parietals each bordered by a single upper secondary temporal scale and single nuchal scale; primary temporal usually single (mostly divided in *S. ruficauda* s.s. and *Sigaloseps ferrugicauda* n. sp.); lower secondary temporal single; tertiary temporals two; postlabials two; nasals moderately to widely separated; anterior loreal higher than wide; supraciliaries usually 7; upper labials 7 with the fifth subocular and contacting the lower eyelid or separated by a complete row of subocular scales; postmental contacting first and second lower labial; transversely enlarged chinshields three, first pair in broad contact, second pair separated by one scale, third pair separated by three scales; *basal scales of 3rd and 4th fingers usually fused to form a single broad scale.

Osteology. Premaxillary teeth 11; *atlantal arches of first cervical vertebrae fused dorsally to each other and to the intercentrum (examined for type species only); presacral vertebrae generally 29; phalangeal formula for the manus 2.3.4.5.3 and for the pes 2.3.4.5.4; two pairs of mesosternal ribs contacting the mesosternum (examined for type species only).

The species of *Sigaloseps* are conservative in morphology with minimal diagnostic differentiation in body proportions or scalation (see Sadlier *et al.* 1999), adult females typically have a color and pattern similar to that of juveniles, that is, they retain the juvenile condition, whereas the adult males change in tail coloration and often also develop a different ventral coloration to that of adult females.

RECOGNIZED SPECIES — *Sigaloseps deplanchei* (Bavay) sensu stricto, *Sigaloseps conditus* n. sp., *Sigaloseps pisinnus* n. sp., *Sigaloseps ruficauda* Sadlier & Bauer, *Sigaloseps ferrugicauda* n. sp., *Sigaloseps balios* n. sp.

Sigaloseps deplanchei (Bavay, 1869)

Figures 2-4

Lygosoma deplanchei Bavay, 1869: 23.

Hinulia tetragonurus Günther, 1872: 420.

Sigaloseps deplanchei (Bavay, 1869) – Sadlier 1986: 50.

TYPE MATERIAL — **Lectotype** *Lygosoma deplanchei* Bavay. BM 86.9.16.1 designated by Sadlier (1986) from two original syntypes (BM 86.9.16.1-2) in the British Museum (BM) listed by Boulenger (1887) as from ‘New Caledonia’ and presented by M.A. Bavay. The lectotype is an adult male; size 42 mm SVL; tail length 32 mm, regenerated; midbody scale rows 28; dorsal scale rows 50; lamellae of fourth toe 26/27. The snout-vent length and the values for scalation characters fall within the range of variation for both *Sigaloseps deplanchei* s.s. or *Sigaloseps conditus* n. sp. The condition of the lower eyelid is that of a transparent ‘window’ or ‘disc’ with fine sutures at the anterior and posterior margins, and the contact with the subocular upper labial is difficult to discern, other than it appears to have a poorly developed row of subocular scales. The description of *Lygosoma deplanchei* by Bavay alludes to the species being found at more than one locality, including the summit of forested mountains, but gives no indication of any specific locality. A series of four syntypes discovered in the Paris Museum were listed a year before Sadlier’s paper (1986) by Brygoo (1985). Three of these specimens have been examined, one is in extremely poor condition, the remaining two have a snout-vent length of 39.0 and 35 mm. The values for scalation characters for these syntypes fall within the range of *Sigaloseps deplanchei* s.s. or *Sigaloseps conditus* n. sp., although there is no obvious complete subocular of scales between the upper labials and lower eyelid and the condition of the lower eyelid is that of a transparent window with the right eyelid of one individual having a fine suture at the posterior margin of the disc.

Holotype *Hinulia tetragonurus* Günther. BM 71.4.16.42 the single syntype in the British Museum listed by Boulenger (1887) as from ‘New Caledonia’ and presented by J. Brenchley Esq., and later identified as the holotype by monotypy by Sadlier (1986). The holotype is an adult male; size 44 mm SVL; tail length 31 mm, regenerated; midbody scale rows 28;

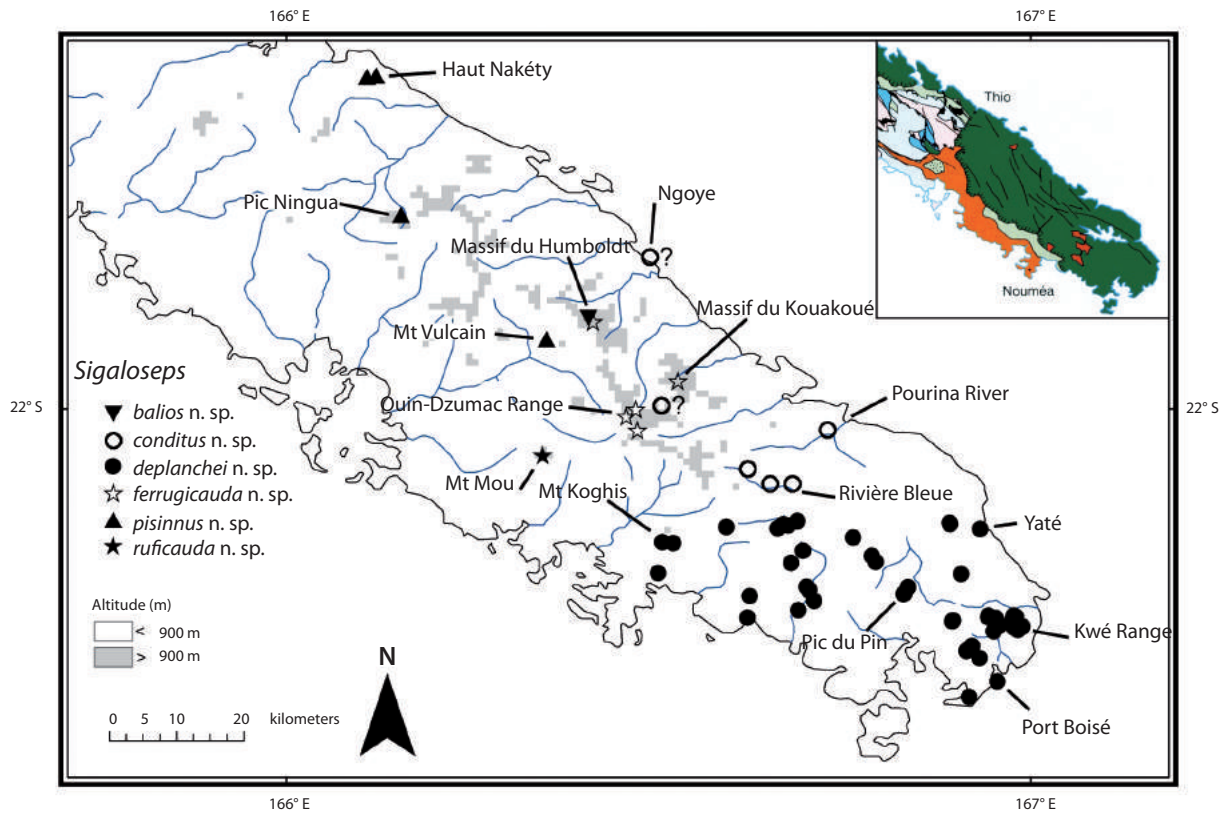


FIGURE 2

Distribution of the species and populations of *Sigaloseps* in southern New Caledonia: *Sigaloseps deplanchei* (Bavay) sensu stricto (closed circle), *Sigaloseps conditus* n. sp. (open circle), *Sigaloseps pisinnus* n. sp. (closed triangle), *Sigaloseps ruficauda* Sadlier and Bauer (closed star), *Sigaloseps ferrugicauda* n. sp. (open star), *Sigaloseps balios* n. sp. (closed inverted triangle) - inset shows extent of ultramafic surfaces (green) in southern region.

dorsal scale rows 50; lamellae of fourth toe 26/26. The snout-vent length and values for scalation characters fall within the range of *Sigaloseps deplanchei* s.s. or *Sigaloseps conditus* n. sp. However, there is no obvious complete subocular of scales between the upper labials and lower eyelid and the condition of the lower eyelid is that of a transparent window with the right eyelid divided by a fine suture medially and at the anterior and posterior margins of the disc.

No single morphological character examined is able to unequivocally assign the types of *Lygosoma deplanchei* Bavay or *Hinulia tetragonurus* Günther to the taxa identified in the genetic study. As such the lectotype of *Lygosoma deplanchei* Bavay (and syntypes) and the holotype of *Hinulia tetragonurus* Günther are not inconsistent with *Sigaloseps deplanchei* s.s. as recognised here, and there is no convincing evidence to indicate that either of the primary types is conspecific with species described here as *Sigaloseps conditus* n. sp. For this reason we adopt a conservative approach and treat the lectotype of *Lygosoma deplanchei* Bavay and holotype of *Hinulia tetragonurus* Günther as conspecific with the widespread taxon in the southern New Caledonia. Further, our investigations into the stay of the vessel H.M.S. *Curaçoa* in New Caledonia, during which journey the type of *Hinulia tetragonurus* was collected, indicate that aside from a one-day stop on the south coast of the island it was otherwise anchored in Nouméa (Brenchley 1873). As such, for the purpose of this review we regard Nouméa or its environs as most likely being the origin of Bavay's types of *Lygosoma deplanchei* and

Günther's holotype of *Hinulia tetragonurus*, and use the large sample from Mt Koghis, in the ranges close to Nouméa, as the benchmark for comparison of *Sigaloseps deplanchei* s.s. with other species and in discussing intraspecific variation.

MATERIAL EXAMINED — Mt Koghis 22°10'43"S 166°30'20"E; R.144349, Aug. 1994; R.146546-60, R.146576-84, 15 Jan. 1995 (all AMS).

DIAGNOSIS — The following features of coloration and scalation in combination will distinguish *Sigaloseps deplanchei* s.s. from all other species of *Sigaloseps* (except *S. conditus* n. sp.): small adult size, maximum SVL of 46 mm for males and 45 mm for females; subocular upper labial usually in contact with the lower eyelid; paravertebral scale rows 49-56; 4th toe lamellae scales 23-28; tail length ~100%SVL; underside of body and tail yellow and without obvious brown or black markings; dorsal and lateral surface of tail usually brown to dull orange. *Sigaloseps deplanchei* s.s. is most similar in morphology to *Sigaloseps conditus* n. sp., with no obvious differences in scalation other than the absence of a well developed row of subocular scales in most *S. deplanchei*.

These characters allow *Sigaloseps deplanchei* s.s. to be distinguished from its congeners as follows:

- from *Sigaloseps conditus* n. sp. in having the subocular upper labial usually in contact with the lower eyelid (vs separated from the lower eyelid by a well developed row of subocular scales).
- from *Sigaloseps pisinnus* n. sp. by its larger adult size (maximum SVL 46 vs 38 mm), shorter tail (mean = ~100% vs 126% of SVL), a duller overall tail color (usually brown to dull orange vs bold reddish-brown), and in having a uniformly pale underside to the tail (vs spotted with small brown blotches).
- from *Sigaloseps ruficauda* by its smaller adult size (maximum SVL 46 vs 60 mm), fewer paravertebral scales (49-56 vs 53-60), shorter tail (mean ~100% vs 150% of SVL) and duller overall color to the tail (usually brown to dull orange vs bright reddish).
- from *Sigaloseps ferrugicauda* n. sp. by its smaller adult size (maximum SVL 46 vs 60 mm), fewer paravertebral scales (49-56 vs 53-60).
- from *Sigaloseps balios* n. sp. by its smaller adult size (maximum SVL 46 vs 50 mm), shorter tail (mean = ~100% vs 128% of SVL), paler yellow ventral coloration (dull yellow vs bold enamel yellow, and paler tail color (usually brown to dull orange vs nearly black).

The genetic data provides strong support for the monophyly of a widespread *Sigaloseps deplanchei* s.s., which is strongly differentiated from all its congeners (see Table 1). In particular, it places *Sigaloseps deplanchei* s.s. within a well supported subgroup that includes the species in the *S. ruficauda* group as its sister, rather than with the morphologically similar *Sigaloseps conditus* n. sp.

DESCRIPTION — The species is re-described from 13 adult males and 12 adult females from Mt Koghis, tests for sexual dimorphism in scalation found no significance differences for the scalation characters surveyed.

Measurements (adults only). Size 39-46 mm SVL; distance from axilla to groin 53.5-59.0% SVL (mean = 56.3); distance from forelimb to snout 37.0-41.9% SVL (mean = 38.9); hindlimb length 28.6-35.7% SVL (mean = 31.7); tail length of individual with most complete tail 107.1% SVL.

Scalation (all specimens). Midbody scale rows 26-30 (mean = 28.0, sd = 0.64); dorsal scale rows 49-56 (mean = 52.4, sd = 1.85); scales on top of fourth finger 8-9 (mean = 8.1, sd = 0.26); lamellae beneath fourth finger 11-14 (mean = 12.1, sd = 0.87); scales on top of fourth toe 10-12 (mean = 11.2 sd = 0.43); lamellae beneath fourth toe 23-28 (mean = 26.0, sd = 1.50).

Osteology. Presacral vertebrae 29.

Color and Pattern. Dorsal surface of body light to mid-brown. Most dorsal scales with a cluster of minute dark spots to the lateral and posterior edges of each scale, giving a dull and clouded appearance to each scale, in some individuals these markings forming dark flecks either positioned medially and running down the center of each scale or to either side of each scale. Upper lateral surface is similar in color to the dorsal surface, progressively grading in tone to a neutral cream color approaching the venter. Most adult females and some adult males with dark markings on the upper lateral surface, in females tending to coalesce and form a dark, broken, dorsolateral streak anteriorly from behind the eye to the

level of the forelimb. Side of the head is similar in color to dorsal surface, with dark markings to the labial and temporal scales and dark streak from the nasal to front of the eye. Tail above and at the sides is similar in color and pattern of dark markings as the body. In life the ventral surface of the body is pale yellow and throat pale grayish white in adult females, and in adult males (Figure 4) moderate yellow on the body and with a bright orange throat, whereas juveniles are grayish white overall. Adult males have a dull (occasionally bold) reddish flush overall to the tail.

Variation. The genetic data indicates the existence of three well supported and differentiated regionally discrete sub-groups within the widespread *Sigaloseps deplanchei* s.s. from southern Grande Terre each comprising two or more populations, and a one sub-group represented by a single population:

- a 'western' group represented by samples from Mt Koghis (northwest) south to Rivière des Pirogues and extending east to Rivière Blanche and Pic du Pin.
- a 'eastern' group represented by samples from Yaté on the east coast and extending inland to Grand Lac (Ka Yé Wagwé).
- a 'southern' group represented by samples south of the Grand Lac and Lac en Huit.
- a localized group in the southeast of the region represented by samples from the Kwé Range.

The sampling of *Sigaloseps deplanchei* in the Grande Sud is reasonably extensive, and has allowed us to identify the existence of the four subgroups. This level of differentiation was unexpected, although an earlier examination of geographical variation in scalation (Sadlier & Bauer 1999) identified significant differences in several characters between 'western' samples represented by the mid-elevation population on Mt Koghis and the 'eastern' (represented by the Goro population) and 'southern' (represented by the Forêt Nord population) groups. This is confounded by the presence of significant differences in several characters between the mid-elevation population on Mt Koghis and the (albeit small) population at the base of the Koghis range.



FIGURE 3

Adult male *Sigaloseps deplanchei* s.s. from the Creek Pernod.



FIGURE 4

Throat and chin coloration of adult male (left) and adult female (right) *Sigaloseps deplanchei* s.s. from the Goro Plateau.

The subgroups of *Sigaloseps deplanchei* in the Grande Sud come into close proximity around the Plaine des Lacs region, and it is difficult to think what factors could be maintaining the discreteness of the genetic groups where they approach each other. The ‘eastern’ subgroup is separated from the ‘western’ and ‘southern’ subgroups by the Rivière des Lacs, Lac en Huit, Grand Lac and the marshes associated with these water bodies, and from the Kwé Range group by the Kwé Binyi River.

DISTRIBUTION AND BIOLOGY — *Sigaloseps deplanchei* has a widespread distribution across the Grande Sud of New Caledonia where it is confined to habitats on ultramafic surfaces (Figure 2). It occurs primarily in forested habitats including humid forest or canopied maquis (maquis preforestier and maquis paraforestier), extending into adjacent low-canopied maquis, open maquis or even wetland maquis where a suitably moist environment exists at ground level. It has not been recorded from areas of extensive open maquis shrubland on lateritic soils, or open maquis on a cuirasse rock surface distant from forest habitat. It occurs in the region as a number of scattered and isolated populations.

COMMENTS — Previous assessments of the distribution of *Sigaloseps deplanchei* have been composite. Samples from Pic Ningua in the far north of the southern ultramafic region are now known to represent *Sigaloseps pisinnus* n. sp., while specimens from the headwaters of the Ni River in the central mountain chain and those collected by Roux & Sarasin in 1911 (Roux 1913) from Ngoye [=Ngoi] and Yaté on the east coast (see Sadlier & Bauer 1999: 88 fig.6;) are more consistent in morphology with *Sigaloseps conditus* n. sp., than with *Sigaloseps deplanchei* s.s.

The specimens collected by Roux & Sarasin from Yaté and assigned to *Sigaloseps deplanchei* by Sadlier (1986) have a complete subocular row of scales and a secondarily scaled (= divided disk) lower eyelid, traits characteristic of *Sigaloseps conditus* n. sp. However, samples from recent collections made at Wao (3 km S Yaté) and at the Yaté Barrage Botanical Reserve (1 km NE Yaté) nested within *Sigaloseps deplanchei* s.s. in the genetic study and are morphologically consistent with that species as recognised here. As such the identity of the Roux & Sarasin specimens from Yaté is unclear. It is possible that both *Sigaloseps deplanchei* s.s. and *Sigaloseps conditus* n. sp. occur in close proximity around Yaté. Such a scenario occurs in the Parc de la Rivière Bleue where *Sigaloseps deplanchei* s.s. is recorded from several sites in the upper reaches of Rivière Blanche and *Sigaloseps conditus* n. sp. from the adjacent upper reaches of Rivière Bleue, the two taxa being separated by a straight line distance of 6 km and a series of intervening ridges to ~500 m elevation with no obvious barriers to contact between the species.

The two specimens collected by Roux & Sarasin from Ngoye and assigned to *Sigaloseps deplanchei* by Sadlier (1986) and a single specimen collected recently from the Ni River in the central mountain chain are more consistent in morphology with *Sigaloseps conditus* n. sp. rather than *Sigaloseps deplanchei* s.s.. As such, it would appear that the northern limit of *Sigaloseps deplanchei* s.s. lies along a boundary that extends from the Dumbéa Valley on the west coast to the upper reaches of Rivière Blanche in the central mountain ranges to Yaté on the west coast, although the boundary on the west coast might extend further north.

CONSERVATION STATUS — Although known from a number of locations a redefined *Sigaloseps deplanchei* has an estimated extent of occurrence of less than 1000 km² and area of occupancy less than 500 km². The genetic data indicates the species comprises three, possibly four, distinct historical lineages, each of which could constitute a separate management unit. In the southern parts of the species' range it occurs on forested habitats across the Goro Plateau including tall canopied maquis (preforestier and paraforestier), and sometimes extends into adjacent low canopied maquis. The ability of the species to occupy a diversity of maquis habitats in this region is reliant on the presence of the extensive broken cap of cuirasse rock which underlies these habitats and provides a humid sub-surface microclimate in an otherwise suboptimal environment. However, these areas of cuirasse typically overlay nickel bearing soils which are now being developed or are under lease for exploitation. As such, there is the potential for extensive parts of the species' extent of occurrence to be reduced by mining activities. In the north and west of its range the species is likely to be restricted to humid forest given that much of this area is covered with lateritic soils that lack the cuirasse rock cap. Here humid forest habitat is highly fragmented and continues to be reduced in area by the impact of firing on the forest edge (*i.e.* Montagne des Sources). Other threats to this species are similar to those recently identified for the skink *Graciliscincus shonae* (Whitaker & Sadlier 2011), which has the same broad distribution, and included threats to habitat quality by introduced ungulates (deer and pigs) damaging the litter layer and disrupting cover (such as rocks and logs), and an adverse impact from the presence of the introduced ant *Wasmannia auropunctata* on populations inhabiting low to mid-elevation forests. Recent survey work across a range of habitats on the Goro Plateau and in reserves elsewhere in the Grande Sud indicate *Sigaloseps deplanchei* is still moderately abundant where it occurs, but that the threats identified above are reducing the species area of occupancy, and as such, on IUCN criteria (IUCN 2001) it would now be considered Near Threatened with the possibility of moving to a higher level of threat with escalated loss of area of occupancy.

Sigaloseps conditus Sadlier, Bauer & Wood, n. sp.

Figures 2, 5, 6

TYPE MATERIAL — Holotype: New Caledonia, MNHN 2011.0284 (formerly AMS R.147952) Rivière Bleue, 4.7 km east of Pont Germain 22°06'S 166°41'E (collected R. Sadlier & G. Shea, 21 Sep. 1995). Paratypes: AMS R.125824, AMS R.125899 Rivière Bleue, Giant Kauri 22°06'S 166°39'E (collected H. Cogger & R. Sadlier, 25 Aug. 1987); AMS R.125895 Rivière Bleue, 1 km East of Giant Kauri 22°06'S 166°39'E (collected H. Cogger & R. Sadlier, 25 Aug. 1987); AMS R.135609-11 Rivière Bleue, vicinity of Giant Kauri 22°06'S 166°40'E (collected A. Greer, 24 Dec. 1988); AMS R.147916 Rivière Bleue, Haute Rivière Bleue Walk 22°05'S 166°37'E (collected R. Sadlier & G. Shea, 20 Sep. 1995); AMS R.147953 Rivière Bleue, 4.7 km East of Pont Germain 22°06'S 166°41'E (collected R. Sadlier & G. Shea, 21 Sep. 1995); AMS R.171426 Pourina River Valley 22°01'39"S 166°43'37"E (collected R. Sadlier, 13 Nov. 2008).

ETYMOLOGY — The species epithet *conditus* is Latin for hidden or secret, and alludes to its unsuspected existence prior to the genetic studies undertaken here.

DIAGNOSIS — The following features of coloration and scalation in combination will distinguish *Sigaloseps conditus* n. sp. all other species of *Sigaloseps* except *S. deplanchei* s.s.: small adult size, maximum SVL for males 44 mm and for females 46 mm; short tail ~100% of SVL; subocular upper labial usually separated from the lower eyelid by a well developed row of subocular scales; midbody scale rows 26-28; paravertebral scale rows 48-52; 4th toe lamellae scales 25-29; underside of body and tail pale yellow without obvious brown or black markings and underside of tail without dark markings; dorsal and lateral surface of tail brown to dull orange.

Sigaloseps conditus n. sp. is most similar in overall appearance to *Sigaloseps deplanchei* s.s. from which it can be usually be distinguished in having a well developed row of subocular scales separating the lower eyelid from the subocular upper labial (vs subocular upper labial usually in contact with the lower eyelid). This character state will also distinguish *S. conditus* n. sp. from all other members of the genus.

The suite of character states identified above allows *Sigaloseps conditus* n. sp. to be distinguished from its congeners as follows:

- from *Sigaloseps pisinnus* n. sp. by its larger adult size (maximum SVL 46 vs 38 mm), significantly more midbody scale rows (26-28 vs 22-24), significantly more toe lamellae (25-29 vs 20-25), duller overall color to the tail (brown vs bold reddish-brown), and in having a uniformly pale underside to the tail (vs spotted with small brown blotches).
- from *Sigaloseps ruficauda* by its smaller adult size (maximum SVL 46 vs 56 mm), significantly fewer paravertebral scales (48-52 vs 53-60), and duller overall color to the tail (brown to dull orange vs bright reddish).
- from *Sigaloseps ferrugicauda* n. sp. by its smaller adult size (maximum SVL 46 vs 60 mm), and significantly fewer paravertebral scales (48-52 vs 53-56).
- from *Sigaloseps balios* n. sp. by its smaller adult size (maximum SVL 46 vs 50 mm), paler yellow ventral coloration (dull yellow vs bold enamel yellow, and paler tail color (brown to dull orange vs nearly black).

The high level of genetic differentiation between *Sigaloseps conditus* n. sp. and the other species in the genus provides strong support for the recognition of these evolutionary lineages as distinct taxa.

DESCRIPTION — The species is described from 3 adult males and 6 adult females.

Measurements. Size 38-46 mm SVL; distance from axilla to groin 50.0-57.1% SVL (mean = 54.2); distance from forelimb to snout 37-42.1% SVL (mean = 39.5); hindlimb length 29.3-34.2% SVL (mean = 31.2); tail length of individual with most complete tail ~100% SVL.

Scalation (all specimens). Midbody scale rows 26-28 (mean = 26.2, sd = 0.67); dorsal scale rows 49-52 (mean = 50.2, sd = 1.30); scales on top of fourth finger 6-8 (mean = 7.6, sd = 0.60); lamellae beneath fourth finger 11-14 (mean = 11.9,



FIGURE 5

Adult male *Sigaloseps conditus* n. sp. (AMS R.125824) from Rivière Bleue.

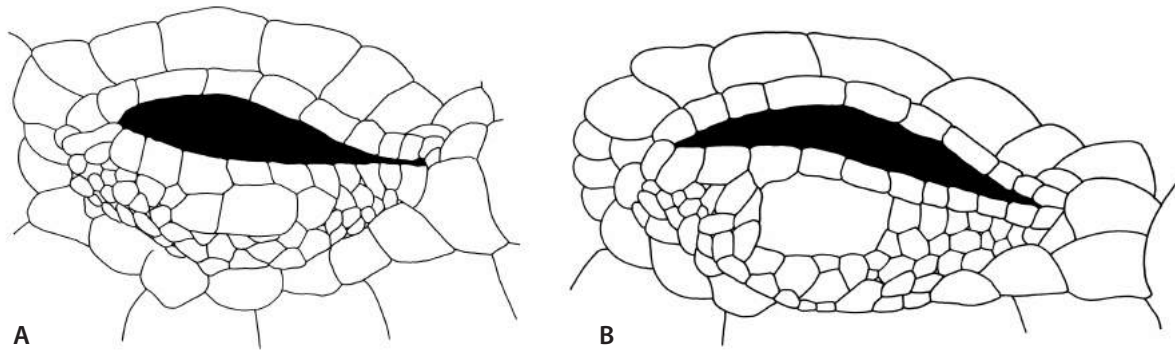
sd = 0.81); scales on top of fourth toe 11-12 (mean = 11.1, sd = 0.33); lamellae beneath fourth toe 26-29 (mean = 26.4, sd = 1.28). Lower eyelid with a semitransparent disc, tending to be divided medially and at the sides by sutures.

Osteology. Pre-maxillary teeth 11 (n = 3); presacral vertebrae 29 (n = 10); manus 2.3.4.5.3 and pes 2.3.4.5.4 (n = 9).

Color and Pattern. Dorsal surface of body light to mid-brown, most (1 in 2 or 2 in 3) dorsal scales with dark flecks usually positioned medially and running down the center of each scale. Upper lateral surface similar in color to dorsal surface but with more intense dark flecking, progressively grading in tone to a neutral cream color approaching the venter, and with the dark markings becoming progressively paler and more obscure in definition on the anterior half of the body. Head similar in color to body, the dark markings usually present as scattered blotches, occasionally more intense on the top of the head, and reducing the paler light to mid-brown base color to a series of enclosed blotches, side of head in the loreal and temporal region similarly marked and the labials predominately dark, with the dark markings on the lower margin of the jaw extending onto the ventro-lateral edge of the throat. Tail with similar dark markings to body above and at the sides, but lacking dark markings to the ventral scales. Ventral surface of the body pale.

Details of Holotype MNHN 2011.0284. Adult male; size 44 mm SVL; tail length 44 mm, near complete. Midbody scale rows 26; dorsal scale rows 50; dorsal scales of fourth finger 7/7; lamellae of fourth finger 12/11; dorsal scales of fourth toe 11/11; lamellae of fourth toe 27/26.

Variation. One individual included in the type series of *Sigaloseps conditus* n. sp. (AMS R.135610) has an incomplete row of subocular scales (both sides) allowing contact between the subocular supralabial scale and lower eyelid. It is assigned to *Sigaloseps conditus* n. sp. on the basis of it being sympatric with two other individuals, each with a complete row of subocular scales, and all three samples being within very close proximity to those used in the genetic studies. However, this does not exclude the possibility that this sample could be an individual of *Sigaloseps deplanchei* and that the two species are syntopic at this location (vicinity of Giant Kaori) at Rivière Bleue.

**FIGURE 6**

Representation of the condition between the lower eyelid in (A) *Sigaloseps conditus* n. sp. (AMS R.147952) showing separation from the subocular upper labial by a complete row of subocular scales and the central area of the lower eyelid divided medially by a fine suture, and the lower eyelid in (B) *Sigaloseps deplanchei* s.s. (AMS R.146553) showing contact between the subocular upper labial and lower eyelid, and the relatively undivided central area of the lower eyelid.

COMMENTS — Specimens from two locations north of Yaté and Rivière Bleue and for which only morphological data are available are consistent in features of scalation with *Sigaloseps conditus* n. sp., rather than *Sigaloseps deplanchei* or *Sigaloseps pisinnus* n. sp., in having a complete subocular row of scales and secondarily-scaled lower eyelid. These include a single specimen from the interior ranges at the headwaters of the Ni River examined in the review of *Sigaloseps deplanchei* by Sadlier & Bauer (1999) and assigned to that species, and two specimens collected by Roux & Sarasin from Ngoye in 1911 (Roux 1913) and examined in the initial review of New Caledonian skinks by Sadlier (1986) and assigned at that time to *Sigaloseps deplanchei*. The single individual from Ngoye assessed for scalation had 28 midbody scale rows and a snout-vent length of 40 mm, also characteristics consistent with *Sigaloseps conditus* n. sp. (rather than *S. pisinnus* n. sp.). As such the distribution of *Sigaloseps conditus* n. sp. is likely extend along the coast and adjacent ranges from the Pourina to the Ngoye River, essentially the Côte Oubliée and its hinterland.

DISTRIBUTION AND BIOLOGY — *Sigaloseps conditus* n. sp. is known from two locations in the ranges of southern Grande Terre at the Pourina River and Rivière Bleue (Figure 2), and likely extends along the Côte Oubliée and its hinterland. The habitat at all sites from which it has been recorded are humid forest on ultramafic substrate.

CONSERVATION STATUS — The distribution of *Sigaloseps conditus* is unclear with the only positive records from Rivière Bleue and the Pourina River, although museum records that could be this species indicate it may extend further to north along the eastern watershed of the Côte Oubliée. As such there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status, and at this time is most appropriately categorized as Data Deficient (DD) under IUCN criteria (IUCN 2001).

Even if the species' distribution elsewhere on the eastern watershed of the Côte Oubliée north of the Pourina River is confirmed its estimated extent of occurrence is still likely to be less than 1500 km² and area of occupancy less than 500 km², making it a candidate for inclusion under one of the higher categories of threat. Its distribution in the region is likely to be highly fragmented given mid- to low-elevation humid forest in this area at has been reduced to small and isolated remnants in river valleys and is only present as more extensive areas at higher elevation around the Humboldt and Kouakoué massifs or as isolated patches on massifs of the southern ultramafic region. Although the catchment of the Pourina River and the rivers to its north are remote, and much of the region is inaccessible, the low- to mid-elevation humid forest remnants in the river valleys lie within extensive areas of maquis vegetation and uncontrolled

fires could significantly reduce the area of forest, particularly of smaller patches with a greater edge to area ratio. As such the species is potentially a candidate for one of the higher threat categories, but further work on determining its extent of occurrence is required.

Sigaloseps pisinnus Sadlier, Shea, Whitaker, Bauer & Wood, n. sp

Figures 2, 7

TYPE MATERIAL — Holotype: New Caledonia, MNHN 2011.0285 (formerly AMS R.171254) Pic Ningua 21°44'20"S 166°09'17"E (collected R. Sadlier & G. Shea, 3 Oct. 2008). Paratypes: AMS R.171249-53, AMS R.171255 same location as holotype (collected R. Sadlier & G. Shea, 3 Oct. 2008); AMS R.172555, AMS R.172576 Mine Galliéni Mt Vulcain, Tontouta Valley 21°54'21"S 166°20'59"E (collected A.H. Whitaker & M. Lettink, 12 Sep. 2009); AMS R.172512-13 Uwëcia, Haut Nakéty, 8 km E Nakéty 21°33'06"S 166°07'14"E (collected A.H. & V.A. Whitaker, 26 June 2009); AMS R.172503-07, AMS R.172514 Chetoré Kwédé, Haut Nakéty, 8 km E Nakéty 21°33'13"S 166°06'31"E (collected A.H. & V.A. Whitaker, 25 June 2009).

ETYMOLOGY — The species epithet comes from the Latin *pisinnus* for small or little, and alludes to the species diminutive size relative to other species of *Sigaloseps*.

DIAGNOSIS — The following features of coloration and scalation in combination will distinguish *Sigaloseps pisinnus* n. sp. all other species of *Sigaloseps*: small adult size, maximum SVL for males and females ~38 mm; subocular upper labial contacting the lower eyelid; paravertebral scale rows 48-55; 4th toe lamellae scales 20-25; underside of body pale yellow and with obvious brown markings along the ventro-lateral surface; dorsal and lateral surface of tail dull to bright orange, the underside with regular dull brown markings (spots) to each scale.

This suite of characters readily distinguishes *Sigaloseps pisinnus* n. sp. from its congeners as follows:

- from *Sigaloseps deplanchei* s.s. by its smaller adult size (maximum SVL 38.5 vs 46 mm) and longer tail (126 vs ~100%); in having significantly fewer midbody scale rows (22-24 vs 24-30, $t_{71} = -11.334$ $P=0.000$); significantly fewer 4th toe lamellae scales (20-25 vs 22-29, $t_{71} = -7.260$ $P=0.000$); a brighter overall color to the tail (bright orange vs usually brown to dull orange), and with the underside to the tail spotted with small brown blotches (vs relatively unmarked).
- from *Sigaloseps conditus* n. sp. by its smaller adult size (maximum SVL 38.5 vs 46 mm) and longer tail (126 vs ~100%) in having the subocular upper labial contacting the lower eyelid (vs subocular upper labial usually separated from the lower eyelid by a well developed row of subocular scales); a brighter overall color to the tail (bright orange vs usually brown to dull orange), and with the underside to the tail spotted with small brown blotches (vs relatively unmarked).
- from *Sigaloseps ruficauda* by its smaller adult size (maximum SVL 38.5 vs 56 mm) and shorter tail (126% vs ~150%); in having significantly fewer midbody scale rows (22-24 vs 26-28); significantly fewer paravertebral scales (48-55 vs 53-60, $t_{71} = -11.334$ $P=0.000$); and with the underside to the tail spotted with small brown blotches (vs relatively unmarked in adults).
- from *Sigaloseps ferrugicauda* n. sp. by its smaller adult size (maximum SVL 38.5 vs 60 mm); in having significantly fewer midbody scale rows (22-24 vs 26-28, $t_{71} = -11.334$ $P=0.000$); significantly fewer paravertebral scales (48-55 vs 53-56, $t_{71} = -11.334$ $P=0.000$); and with the underside to the tail spotted with small brown blotches (vs relatively unmarked in adults).
- from *Sigaloseps balios* n. sp. by its smaller adult size (maximum SVL 38.5 vs 50 mm), in having significantly fewer midbody scale rows (22-24 vs 26-28); significantly fewer paravertebral scales (48-55 vs 53-56); paler yellow ventral coloration (moderate yellow vs bold enamel yellow), and paler tail color (orange vs nearly black).

Sigaloseps pisinnus n. sp. is most similar in morphology to *Sigaloseps deplanchei* s.s. and *Sigaloseps conditus* n. sp. in that it shares a similar dorsal and lateral color pattern, but is readily distinguished from these two species by its smaller

**FIGURE 7**

Adult male *Sigaloseps pisinnus* n. sp. (AMS R.171254 - holotype) from Pic Ningua.

size and longer tail with small brown blotches on the underside. The morphological differentiation between *Sigaloseps pisinnus* n. sp. and the other recognized species in the genus in combination with a high level of genetic differentiation clearly identifies it as an evolutionary lineage warranting recognition as a distinct species.

DESCRIPTION — The species is described from 6 adult males and 9 adult females, and two juveniles, measurements for adults only.

Measurements. Size 33-38 mm SVL; distance from axilla to groin 51.4-57.7% SVL (mean = 55.3); distance from forelimb to snout 36.6-41.2% SVL (mean = 39.3); hindlimb length 31.1-35.3% SVL (mean = 32.7); tail length of individual with most complete tail 139.5% SVL.

Scalation (all specimens). Midbody scale rows 22-24 (mean = 23.9, sd = 0.48); dorsal scale rows 48-55 (mean = 51.6, sd = 2.30); scales on top of fourth finger 6-9 (mean = 7.6, sd = 0.65); lamellae beneath fourth finger 9-11 (mean = 10.0, sd = 0.74); scales on top of fourth toe 10-12 (mean = 11.0, sd = 0.41); lamellae beneath fourth toe 20-25 (mean = 22.9, sd = 1.37).

Osteology. Pre-maxillary teeth 11 (n = 8) - 12 (n = 1); presacral vertebrae 29 (n = 10); manus 2.3.4.5.3 and pes 2.3.4.5.4 (n = 10).

Color and Pattern. Dorsal surface of body light to mid-brown, most dorsal scales with dark flecks either positioned medially and running down the center of each scale or to either side of each scale, the lateral and posterior edges of each scale with a cluster of minute dark spots giving a dull and clouded edge at the back and side of each scale. Upper lateral

surface similar to dorsal surface, progressively grading in tone to a neutral cream color approaching the venter, and with the dark markings becoming progressively paler and more obscure in definition. Ventral surface of the body pale and with the dark markings on the lateral surface occasionally extending onto the ventro-lateral edge. Head darker overall in appearance, the dark markings dominating and forming a reticulate pattern over the scales on the top of the head, in effect reducing the paler light to mid-brown base color to a series of enclosed blotches, side of head in the loreal and temporal region similarly marked, labials predominately dark and with the dark markings of the lower jaw extending onto the ventro-lateral edge of the throat. Tail with similar dark markings to the body above and at the sides, and with a pattern of paler dark markings to most scales on the underside. In life the ventral surface of adult males and females has a yellow flush (absent in juveniles) and there is no distinctive color to the throat. One adult male (AM R171254) has a bold reddish flush overall to the tail, whereas this was not as pronounced in adult females. Juveniles had a similar reddish flush to the tail and to the body behind the forelimbs.

Details of Holotype (MNHN 2011.0285, Figure 7). Adult male; size 38.5 mm SVL; tail length 45 mm, regenerated. Midbody scale rows 24; dorsal scale rows 54; dorsal scales of fourth finger 8/9; lamellae of fourth finger 11/11; dorsal scales of fourth toe 11/12; lamellae of fourth toe 23/21.



FIGURE 8

Humid forest on Pic Ningua.

Variation. The genetic data indicates the presence of significant regional sub-structuring within *Sigaloseps pisinnus* n. sp., with all three known populations genetically discrete and with high levels of support for the monophyly of each. There is also strong support for a relationship between the two northern populations (Nakéty and Pic Ningua). No significant differences in scalation were detected between two northern populations, and there are too few individuals from the southern population (Tontouta valley) for statistical comparison.

ADDITIONAL MATERIAL EXAMINED — R.174959 Camp des Sapins 21°47'36"S 166°9'31"E; R.174955 Camp des Sapins 21°45'23"S 166°11'46"E; R.174956 Camp des Sapins 21°47'46"S 166°9'42"E; R.174957 Camp des Sapins 21°45'44"S 166°11'44"E; R.174960 Camp des Sapins 21°46'42"S 166°10'29"E; R.174958 Camp des Sapins 21°47'36"S 166°9'31"E; R.174968 Pic Ningua, ridge between Cidoa and Pic Ningua 21°44'36"S 166°10'43"E; R.174979 Pic Ningua, ridge between Cidoa and Pic Ningua 21°44'21"S 166°11'5"E - all collected A.H. & V.A. Whitaker, 8-15 November 2011 (all AMS) but not included in the type series.

DISTRIBUTION AND BIOLOGY — *Sigaloseps pisinnus* n. sp. is known from three locations, all on ultramafic surfaces (north to south): two sites in closed-forest remnants at around 500 m on the Haut Nakéty plateau of the near coastal ranges of the central-east region between Canala and Thio; multiple sites in mid- to high-elevation forest (Figure 8) and maquis between 400-1100 m on the Mt Cidoa-Pic Ningua-Koungouhaou Nord massif on the main axial range of the southern region between Thio and Bouloupari; and mid-elevation closed-forest at around 500 m at Mine Galliéni, on Mt Vulcain in the interior of the southern region ranges of the Tontouta valley (Figure 2).

Sigaloseps pisinnus n. sp. is exceptional amongst the *Sigaloseps* species for its occurrence in open maquis habitats. At Camp des Sapins this species was one of the most common skink species in sparse maquis on rocky ultramafic surfaces, including cuirasse.

The population from Pic Ningua is located at the northern edge of the main southern ultramafic block that covers much of the southern region. The area of ultramafic surfaces that include the coastal ranges of the Nakéty population are continuous with the extensive ultramafic surfaces to the south, but not with nearby areas of ultramafic surface to the north. *Sigaloseps pisinnus* n. sp. has not been recorded from ultramafic surfaces of the central-east region north of Nakéty that include coastal and interior ranges, despite extensive survey work in this area, and as such the break in the ultramafic surfaces between these regions may represent an historical barrier to dispersal for this group of lizards.

CONSERVATION STATUS — *Sigaloseps pisinnus* n. sp. is known from three geographically distant locations, two in the southern ultramafic region and one on ultramafic surfaces of the adjacent central-east region, and has been recorded from both high and mid-elevation. The species' extent of occurrence is unclear as only limited survey work has been undertaken in intervening areas that would give an indication as to the likely continuity of distribution across its range. Regardless, its estimated extent of occurrence is still likely to be considerably less than 1500 km² and area of occupancy less than 500 km². Humid forest in the southern ultramafic region at mid- to low-elevation has been reduced to small and isolated patches in river valleys and subject to a range of threats that includes wildfires, mining, microhabitat damage by introduced ungulates (including in reserves) and the spread of the introduced ant *Wasman-nia auropunctata* in low to mid-elevation forests. A similar scenario exists for forests on the ultramafic surfaces of the east-central region. On the Mt Cidoa-Pic Ningua-Koungouhaou Nord massif the maquis habitats outside the reserves of Réserve Botanique du Pic Ningua are at risk to expansion of mining activities. At this time the species meets the IUCN criteria (IUCN 2011) to be categorized as Endangered (B1, a, biii & B2 a, biii). The species' area of occurrence and area of occupancy is likely to remain under the threshold for a lower level of threat and the species' distribution, even with further sites recorded, is likely to remain severely fragmented by virtue of the distribution of available habitat in the region.

Sigaloseps ruficauda Sadlier & Bauer, 1999

Figures 2, 9

Sigaloseps ruficauda Sadlier & Bauer, 1999: 84.

MATERIAL EXAMINED — AMS R.146482 (holotype), AMS R.146196-97, MNHN 1997.3326 Mt. Mou 22°03'45"S 166°20'39"E; AMS R.146481 and AMS R.146483 Mt. Mou 22°04'01"S 166°20'34"E; AMS R.148004 Mt. Mou 22°03'42"S 166°20'41"E.

DIAGNOSIS — The following features of coloration and scalation in combination will distinguish *Sigaloseps ruficauda* from all other species of *Sigaloseps* (except *S. ferrugicauda* n. sp.): moderately large adult size, maximum SVL for females 47 mm; subocular upper labial usually in contact with the lower eyelid; paravertebral scale rows 53-60; 4th toe lamellae scales 21-28; underside of body and tail yellow without obvious brown or black markings; dorsal and lateral surface of tail bright orange. *Sigaloseps ruficauda* is very similar in morphology to *Sigaloseps ferrugicauda* n. sp. with no obvious differences in scalation and only subtle differences in intensity of tail coloration and dark markings on the upper surfaces of the tail. As such, recognition of these taxa as each comprising a distinct evolutionary lineage draws heavily on the high level of genetic differentiation between them.

The suite of diagnostic characters identified above will allow *Sigaloseps ruficauda* to be distinguished from each of its congeners as follows:

- from *Sigaloseps deplanchei* s. s. by its larger adult size (maximum SVL 56 vs 46 mm) and longer tail (150% vs 100%), more paravertebral scales (53-60 vs 46-56), and bolder overall color to the tail (bright reddish vs usually brown to dull orange).
- from *Sigaloseps conditus* n. sp. by its larger adult size (maximum SVL 56 vs 46 mm) and longer tail (150% vs ~100%), more paravertebral scales (53-60 vs 48-52), in having the subocular upper labial usually in contact with the lower eyelid (vs usually separated from the lower eyelid by a well developed row of subocular scales), and bolder overall color to the tail (bright reddish vs brown to dull orange).
- from *Sigaloseps pisinnus* n. sp. by its much larger adult size (maximum SVL 56 vs 38 mm), longer tail (150% vs 126%), in having significantly more midbody scale rows (26-28 vs 22-24); significantly more paravertebral scales (53-60 vs 48-55); and bolder overall color to the tail (bright reddish vs bold reddish-brown) with the underside to the tail relatively unmarked (vs spotted with small brown blotches).
- from *Sigaloseps ferrugicauda* n. sp. by its bolder overall color to the tail (bright reddish vs dull russet brown) and lack of dark markings on the upper surfaces of the tail (vs dark markings variably present).
- from *Sigaloseps balios* n. sp. by its larger adult size (maximum SVL 56 vs 46 mm), longer tail (150% vs 128%), paler ventral coloration (moderate yellow vs bold enamel yellow), and paler tail color (bright reddish vs nearly black).

DESCRIPTION — The species is described from one adult male, two adult females and one subadult female, and three hatchlings.

Measurements. (n = 4) for adults and subadult: 38-56 mm SVL; distance from axilla to groin 55.3-58.3% SVL (mean = 55.9); distance from forelimb to snout 35.7-39.6% SVL (mean = 38.1); hindlimb length 30.4-36.8% SVL (mean = 33.7); tail length of individual with most complete tail ~152.6% SVL. Tail length for three hatchling juveniles 129.6-144.0% SVL (mean = 137.0%).

Scalation. All specimens n = 7: midbody scale rows 26-28 (mean = 26.6, sd = 0.98); dorsal scale rows 53-60 (mean = 55.6, sd = 2.30); scales on top of fourth finger 7-9 (mean = 8.1, sd = 0.75); lamellae beneath fourth finger 9-15 (mean = 11.8, sd = 0.80); scales on top of fourth toe 10-13 (mean = 11.1, sd = 1.10); lamellae beneath fourth toe 21-28 (mean = 24.7, sd = 1.95).

Osteology. Maxillary teeth 11 (n = 2); presacral vertebrae 29 (n = 6); postsacral vertebrae 47 (n = 3) and 49 (n = 1); manus 2.3.4.5.3 and pes 2.3.4.5.4 (n = 5).

Color and Pattern (Figure 9). Dorsal surface of body of adults mid to dark brown, most dorsal scales with dark flecks either positioned medially with the long axis running down the center of each scale or to one side of the scale. Dorsolateral edge with a dark bar between the eye and naris, continuing from the posterior edge of the eye and bordered above by a pale stripe (~1 scale width, with a russet tinge in life and bordered by a dark edge above) to just past the forelimbs. Side of body similar to dorsal surface uppermost but progressively grading in tone to a neutral cream color and with fewer and more scattered dark markings approaching the venter. Ventral surface of the body pale and with the dark markings on the lateral surface occasionally extending onto the ventro-lateral edge. Head with a pattern of dark spots and irregular blotches over the scales on the top of the head, side of head in the loreal and temporal region similarly marked, and the labials also with bold dark markings that extend onto the ventro-lateral edge of the throat. Tail lacking dark markings and with a bold, reddish flush overall in life.

The dorsal and lateral surfaces of the body of the single subadult (a female - incorrectly cited as an adult male by Sadlier & Bauer 1999) light brown and lacking obvious dark markings, and in life had a dull reddish suffusion to the anterior part of the body and reddish flush to the tail with brownish markings underneath.

Details of Holotype. Adult female; size 56 mm SVL; tail length 64 mm, regenerated. Midbody scale rows 26; dorsal scale rows 58; dorsal scales of fourth finger 9/9; lamellae of fourth finger 13/12; dorsal scales of fourth toe 12/12; lamellae of fourth toe 25/25.



FIGURE 9

Adult female *Sigaloseps ruficauda* Sadlier & Bauer (AMS R.146483) from Mt Mou.

DISTRIBUTION AND BIOLOGY — *Sigaloseps ruficauda* is known only from high-elevation habitats on Mt Mou on the southwest coast (Figure 2). The Mt Mou massif rises to 1200 m from the west coast plain, it lies approximately 12 km from Mt Ouin, the type locality for *Sigaloseps ferrugicauda* n. sp., and is connected to the interior massifs by a range that rarely falls below 800 m in elevation.

The species is recorded from high-elevation maquis habitat (~1100 m) adjacent to humid forest habitat. The maquis had a very dense understory of fern (*Gleichenia*), an indication that this habitat had been frequently burned and was highly disturbed. In retrospect it is considered highly likely the species also occurs in forest habitat and that its occurrence in the adjacent maquis is an artifact of proximity and its dense understory of ferns which provide a sufficiently cool and moist environment for the species to exist there, rather than as the preferred habitat type.

CONSERVATION STATUS — *Sigaloseps ruficauda* is known from a single site within La Réserve Naturelle du Mont Mou near the summit area of Mt Mou. This very restricted distribution indicates an extent of occurrence and area of occupancy of <5 km². The greatest threat to *S. ruficauda* is further habitat destruction leading to a reduction in the area of occupancy. The degraded maquis vegetation on the slopes of Mt Mou is indicative of frequent burning and this leads to habitat loss, primarily from the forest edge, due to encroachment from fires in adjacent maquis shrubland. Introduced ungulates (deer and pigs) also threaten habitat quality, particularly by damaging the litter layer. Given the species' extremely restricted distribution and the threats it faces, particularly from fire, it is most appropriately categorized as Vulnerable (D2) under IUCN criteria (IUCN 2011).

Sigaloseps ferrugicauda Sadlier, Smith, Shea & Bauer, n. sp.

Figures 2, 10

HOLOTYPE — MNHN 2011.0286 (formerly R.165803) Mt Ouin, track along northeast edge of Mt Ouin Range 22°00'S 166°28'E (collected R. Sadlier & G. Shea, 26 Dec. 2003).

PARATYPES — AMS R.148024 Mt Ouin 22°34'S 166°27'26"E (collected R. Sadlier & G. Shea, 26 Sep. 1995); AMS R.162964 Mt Ouin, saddle between Mt Ouin and Mt Dzumac 22°01'41"S 166°28'19"E (collected R. Sadlier & A. Bauer, 19 Sep. 2002); AMS R.172611 Massif du Humboldt 21°52'57"S 166°34'45"E at 1350 m (collected R. Sadlier & C. Beatson, 13 Oct. 2009).

ETYMOLOGY — The species epithet is from the Latin *ferrugineus* for rust-colored, and *cauda* for tail, alluding to the dull russet tail coloration of this species.

DIAGNOSIS — The following features of coloration and scalation in combination will distinguish *Sigaloseps ferrugicauda* n. sp. from all other species of *Sigaloseps* (except *S. ruficauda* s.s.): moderately large adult size, maximum SVL for females 60 mm; subocular upper labial usually in contact with the lower eyelid; paravertebral scale rows 53–56 (mean = 54.5); 4th toe lamellae scales 24–28 (mean = 26.1); underside of body and tail yellow without obvious brown or black markings; dorsal and lateral surface of tail dull russet brown and with dark markings variably on the upper surfaces of the tail. *Sigaloseps ferrugicauda* n. sp. is most similar in morphology to *Sigaloseps ruficauda*, with no obvious differences in scalation and only a subtle difference in intensity of reddish tail coloration and of dark markings on the upper surface of the tail. The high level of genetic differentiation between *Sigaloseps ferrugicauda* n. sp. and *Sigaloseps ruficauda* provides strong support for the recognition of these evolutionary lineages as distinct taxa.

The suite of diagnostic characters identified above allows *Sigaloseps ferrugicauda* n. sp. to be distinguished from each of its congeners as follows:



FIGURE 10

Adult female *Sigaloseps ferrigicauda* n. sp. (AMS R.165803) from Mt Ouin (A), and ventral surface (B).

- from *Sigaloseps deplanchei* s.s by its larger adult size (maximum SVL 60 vs 46 mm), more paravertebral scales (53-56 vs 46-56).
- from *Sigaloseps conditus* n. sp. by its larger adult size (maximum SVL 60 vs 46 mm), more paravertebral scales (53-56 vs 48-52), in having the subocular upper labial usually in contact with the lower eyelid (vs separated from the lower eyelid by a well developed row of subocular scales).
- from *Sigaloseps pisinnus* n. sp. by its larger adult size (maximum SVL 60 vs 38 mm), in having significantly more midbody scale rows (26-28 vs 22-24); more paravertebral scales (53-56 vs 48-55); duller overall color to the tail (dull russet brown vs bold reddish-brown), and in having a relatively uniformly pale underside to the tail (vs spotted with small brown blotches).
- from *Sigaloseps ruficauda* by its duller overall color to the tail (dull russet brown vs bright reddish), and the presence (variably) of dark markings on the upper surfaces of the tail (vs upper surface of the tail unmarked).
- from *Sigaloseps balios* n. sp. by its larger adult size (maximum SVL 60 vs 50 mm), paler ventral coloration (moderate yellow-orange vs bold enamel yellow), and paler tail color (dull russet brown vs nearly black).

DESCRIPTION — The species is described from one adult male and three adult females.

Measurements. Size 54-60 mm SVL; distance from axilla to groin 53.7-56.9% SVL (mean = 55.6); distance from forelimb to snout 36.2-40.0% SVL (mean = 37.6); hindlimb length 30.0-34.7% SVL (mean = 32.3); tail of all specimens with sections either missing or reproduced.

Scalation (all specimens). Midbody scale rows 26-28 (mean = 26.5, sd = 1.00); dorsal scale rows 53-56 (mean = 54.5, sd = 1.29); scales on top of fourth finger 8-9 (mean = 8.25, sd = 0.5); lamellae beneath fourth finger 12-13 (mean = 12.75, sd = 0.5); scales on top of fourth toe 10-12 (mean = 11.1, sd = 0.63); lamellae beneath fourth toe 24-28 (mean = 26.1, sd = 1.34).

Osteology. Pre-maxillary teeth 11 (n = 1); presacral vertebrae 29 (n = 4); postsacral vertebrae unknown; manus 2.3.4.5.3 and pes 2.3.4.5.4 (n = 4).

Color and Pattern. Dorsal surface of body variable, light to mid-brown overall. Darker individuals with the dark flecks on dorsal the scales positioned medially and the long axis running down the center of each scale, or occasionally to one side of the scale. Paler individuals with the dark dorsal markings not well defined or largely absent. Dorsolateral edge with a dark bar between the eye and naris, continuing from the posterior edge of the eye and bordered above by a pale stripe (~1 scale width, with a russet tinge in life and bordered by a dark edge above) to just past the forelimbs. Side of body uppermost duller than dorsal surface but with a similar pattern of dark markings to the dorsal surface, progressively grading in tone (and in those individuals with dark markings these becoming fewer and more scattered) approaching the venter. Ventral surface of the body pale (yellow/orange in life), and the tail duller and with occasional dark spots. Head variably with scattered diffuse dark spots over the scales on the top of the head, but without obvious dark markings on the side of head. Lower labials variably with dark markings, which when present extend onto the ventro-lateral edge of the throat. Tail with a similar intensity of dark markings as the dorsal surface, tending to be more concentrated along the dorsolateral edge, and with a dull russet brown flush overall in life.

Details of Holotype MNHN 2011.0286 (Figure 10). Adult male; size 60 mm SVL; tail length 49 mm, regenerated. Midbody scale rows 26; dorsal scale rows 54; dorsal scales of fourth finger 8/8; lamellae of fourth finger 13/-; dorsal scales of fourth toe 11/11; lamellae of fourth toe 28/27.

DISTRIBUTION AND BIOLOGY — *Sigaloseps ferrugicauda* n. sp. is known from high-elevation habitats on Mt Ouin (1100 m) and Mt Humboldt (1350 m), two mountain peaks in the interior of the central ranges in southern Grande Terre, and a single specimen from the nearby Massif du Kouakoué which is here also assigned to *S. ferrugicauda* n. sp. (but not included in the type series). These three peaks lie approximately 10-15 km from each other in a rough 'V' with Mt Ouin at the southern apex, and are connected by ranges that rarely fall below 1000 m. In turn, Mt Mou, the type locality for *Sigaloseps ruficauda*, lies to the south and west of Mt Ouin by ~15 km along a near continuous range that

drops below 800 m. in elevation for part of this length and rarely rises above 900 m. on remainder of the range between Monts Couvelée and Mt Mou.

CONSERVATION STATUS — *Sigaloseps ferrugicauda* n. sp. is known from several isolated but geographically proximate high-elevation sites in the southern ultramafic region. The extent of occurrence is estimated at approximately 50 km² and the area of occupancy at <5 km². Two sites occur within protected areas, Réserve Naturelle du Mont Humboldt and La Réserve naturelle du Massif du Kouakoué, meaning some protection is afforded, but mineral exploration has occurred at the Mt Ouin in the past and mining activity is currently intensifying in the nearby Tontouta Valley system. The montane forest at all sites is at risk to peripheral damage and reduction in area of occupancy from firing in the adjacent maquis shrubland. Introduced mammals (rodents, cats and pigs) are a potential predation risk and introduced ungulates (deer and pigs) threaten habitat quality, particularly by damaging the litter layer. The species is conservatively categorized as Vulnerable (D2) under IUCN criteria (IUCN 2001) given its extremely restricted distribution, but could be moved to a higher level of threat if faced by increased loss of area of occupancy or decline in area, extent and/or quality of habitat with increased pressure from introduced species.

***Sigaloseps balios* Sadlier, Bauer & Wood, n. sp.**

Figures 2, 11

TYPE MATERIAL — Holotype: New Caledonia, MNHN 2011.0287 (formerly AMS R.172612) Massif du Humboldt 21°52'57"S 166°34'45"E at 1350 m. (collected R. Sadlier & C. Beatson, 13 Oct. 2009). Paratypes: AMS R.172616 Massif du Humboldt 21°52'50"S 166°24'29"E at 1390 m (collected H. Jourdan, 13 Oct. 2009); AMS R.172620-21 Massif du Humboldt 21°52'50"S 166°24'29"E at 1390 m (collected R. Sadlier & C. Beatson, 15 Oct. 2009).

ETYMOLOGY — The species epithet is from the Greek *balios* for dappled, and alludes to the contrasting light and dark coloration on the underside of the tail characteristic of this species.

DIAGNOSIS — The following features of coloration and scalation in combination will distinguish *Sigaloseps balios* n. sp. from all other species of *Sigaloseps*: maximum adult size 50 mm SVL (adult females); subocular upper labial in contact with the lower eyelid; midbody scale rows 26-28; paravertebral scale rows 58-61 (mean = 59.0); 4th toe lamellae scales 23-25 (mean = 24.2); underside of body enamel yellow and underside of tail with large dark spots.

These characters allow *Sigaloseps balios* n. sp. to be distinguished from its congeners as follows:

- from *Sigaloseps deplanchei* s.s. in having more paravertebral scales (58-61 vs 46-56), longer tail (128% vs ~100% SVL), bolder ventral coloration (enamel yellow vs moderate yellow), and darker tail color (nearly black vs dull reddish-brown).
- from *Sigaloseps conditus* n. sp. in having more paravertebral scales (58-61 vs 46-56), the subocular upper labial contacting the lower eyelid (vs separated by a complete row of subocular scales), bolder ventral coloration (enamel yellow vs moderate yellow), and darker tail color (nearly black vs dull reddish-brown).
- from *Sigaloseps pisinnus* n. sp. by its larger adult size (maximum SVL 50 vs 38 mm), significantly more midbody scales (26-28 vs 22-24), significantly more paravertebral scales (58-61 vs 48-55), bolder ventral coloration (enamel yellow vs moderate yellow), and darker tail color (nearly black vs dull reddish-brown).
- from *Sigaloseps ruficauda* by its smaller adult size (maximum SVL 50 vs 56 mm), shorter tail (~128% vs 150%), bolder ventral coloration (enamel yellow vs moderate yellow), and darker tail color (nearly black color vs reddish).
- from *Sigaloseps ferrugicauda* n. sp. by its smaller adult size (maximum SVL 50 vs 60 mm), bolder ventral coloration (enamel yellow vs moderate yellow-orange), and darker tail color (nearly black color vs dull russet brown).

Sigaloseps balios n. sp. is unlikely to be confused with any other species of *Sigaloseps*. In size it is intermediate between the two largest species in the genus, *S. ruficauda* and *S. ferrugicauda* n. sp., and the other species of *Sigaloseps*. It has a



FIGURE 11

Adult female *Sigaloseps balios* n. sp. (AMS R.172612) (A) and ventral surface (B), and subadult female *Sigaloseps balios* n. sp. (AMS R.172621) (C) from Mt Humboldt.

number of scalation and coloration characteristics that will readily distinguish it from *S. deplanchei* sensu stricto, *S. conditus* n. sp. and *S. pisinnus* n. sp. It has an elevated number of paravertebral scales (equal to or greater than 50), a feature shared with *Sigaloseps ruficauda* and *Sigaloseps ferrugicauda* n. sp., but is readily distinguished from these species by marked differences in size and tail and ventral coloration. The genetic data indicate the relationships of *S. balios* n. sp. lie with the other high-elevation endemics *S. ruficauda* and *S. ferrugicauda* n. sp. It shows a high level of genetic differentiation from *S. ferrugicauda* n. sp. with which it is sympatric on Mt Humboldt, but only a low level of differentiation from the allopatrically distributed *S. ruficauda*. However, the morphological differences between *S. ruficauda* and *S. balios* n. sp. provide strong support for the recognition of each as a distinct evolutionary lineage.

DESCRIPTION — The species is described from two adult females (AMS R.172612 & AMS R.172620) and one subadult male (AMS R.172621).

Measurements. Size 40.5–50 mm SVL; distance from axilla to groin 54.2–58.0% SVL (mean = 55.5); distance from forelimb to snout 36–40.7% SVL (mean = 38.1); hindlimb length 33.3–34.6% SVL (mean = 34.0); tail length of individual with most complete tail 128.4% SVL.

Scalation. Midbody scale rows 26–28 (mean = 26.7, sd = 1.15); dorsal scale rows 58–61 (mean = 59.0, sd = 1.73); scales on top of fourth finger 8–9 (mean = 8.5, sd = 0.5); lamellae beneath fourth finger 12–14 (mean = 12.8, sd = 0.74); scales on top of fourth toe 11–12 (mean = 11.2, sd = 0.29); lamellae beneath fourth toe 23–25 (mean = 24.2, sd = 0.76).

Osteology. Pre-maxillary teeth 11 (n = 2); presacral vertebrae 29 (n = 3); postsacral vertebrae unknown; manus 2.3.4.5.3 and pes 2.3.4.5.4 (n = 3).

Color and Pattern. Adult females—dorsal surface of body mid-brown overall with a coppery tinge, scales on the posterior half of the body with darker pigmentation on the anterior and lateral edges of each scale becoming progressively more intense approaching the hindlimbs, eventually covering much of each individual scale on the hips and down the dorsal and lateral surfaces of the tail. Side of body uppermost predominately dark brown to black, with scattered pale markings (mid-brown in color as for dorsal surface), the dark coloration progressively grading in tone and the pale markings increasing in number and covering whole individual scales approaching the venter. Top of head and neck similar in color to body, the head with scattered dark markings on larger scales. Side of neck similar to side of body but more diffuse, and side of the head with scattered light brown interspaces. Dark markings of the anterior part of the body and neck concentrated uppermost and forming a dark dorsolateral stripe that extends from the level of the forelimb to the posterior edge of the eye, and as well defined dark streak between the naris and anterior edge of the eye. Ventral surface of the body moderate to bold enamel yellow in life, not extending to the throat (some extension of the yellow color anterior of the forelimbs). Underside of tail pale (yellowish proximally but becoming white towards tip) with large dark markings to each of the subcaudal and adjacent scales.

Subadult male—dorsal surface of body mid-brown overall with a coppery tinge, scales over the hindlimbs and down the tail, becoming progressively darker on the anterior and lateral edges of each scale. Sides of body and neck a mixture of scattered dark (black in life) and pale spots, darker markings concentrated uppermost, progressively grading in tone and becoming more diffuse approaching the venter. Head and neck similar above in color to body, head without dark markings on larger dorsal head scales. Dark markings on the side of the body, neck and head concentrated uppermost and forming a dark and continuous dorsolateral stripe that extends from the level of the forelimb to the posterior edge of the eye, and between the naris and anterior edge of the eye. Ventral surface of the body and throat pale, with some extension of darker lateral markings onto ventro-lateral region and across the throat. Underside of tail pale and with large dark markings to each of the subcaudal and adjacent scales.

A single poorly preserved juvenile (27.5 mm SVL) was similar in coloration to the subadult male, but had a lighter stripe (~ one scale width) bordering the upper edge of the dark dorsolateral stripe, and the scales of the ventral surface were suffused with dark pigment variably expressed as isolated dark markings on the throat.

Details of Holotype MNHN 2011.0287 (Figure 11). Adult female; size 50 mm SVL; tail length 37.5 mm, distal 20 mm regenerated. Midbody scale rows 26; dorsal scale rows 61; dorsal scales of fourth finger 8/9; lamellae of fourth finger 12/14; dorsal scales of fourth toe 11/12; lamellae of fourth toe 24/24.

DISTRIBUTION AND BIOLOGY — *Sigaloseps balios* n. sp. is known only from high-elevation habitat on the summit area of Mt Humboldt in the interior ranges of southern Grande Terre (Figure 2). The types were collected during a survey of the Réserve Naturelle du Mont Humboldt in October 2009. Conditions during the survey were optimal with warm sunlit days, although nights were cold. The holotype was collected from dense, low maquis shrubland adjacent to high-elevation humid forest (Figure 12) and the paratypes from just inside high-elevation moss forest at its upper altitudinal limit. However, it is important to note that the species was not encountered in the interior of the moss forest despite extensive sampling under optimal conditions over an altitudinal range of 1250–1390 m.

The largest adult female collected in October had a single enlarged ovarian follicle either side, and the slightly smaller female a single large egg.

CONSERVATION STATUS — *Sigaloseps balios* n. sp. is known from a single site near the summit of Mt Humboldt and within La Réserve Naturelle du Mont Humboldt. The extent of occurrence and the area of occupancy are estimated at <5 km². The greatest threat to *S. balios* n. sp. is loss or degradation of habitat leading to a reduction in the area of occupancy. Introduced ungulates (deer and pigs) threaten habitat quality, particularly by damaging the litter layer, and wildfires in adjacent maquis shrubland can degrade the forest edge and reduce the extent of closed forest. Introduced mammals (rodents, cats and pigs) pose a potential predation risk. The species is conservatively categorized as Vulnerable (D2) under IUCN criteria (IUCN 2001) because of its extremely restricted distribution, but could move to a higher threat category if faced with an increased decline in area, extent and/or quality of habitat.



FIGURE 12

Humid forest on Mt Humboldt.

DISCUSSION

Recent investigations have identified the ultramafic massifs of the north-west/central-west and southern regions of Grande Terre as discrete biogeographic regions for skinks, each with a number of endemic taxa. These two regions also account for the majority of localized narrow-range skink species, most restricted to humid forest habitat which is now often only present as isolated remnants. While some of these remnant forests are likely to be the legacy of extensive historical fragmentation their boundaries are now confused by recent human-induced fragmentation. Of particular interest are the species of skink in the genera *Nannoscincus*, *Sigaloseps* and *Marmorosphax* that are found primarily in high-elevation humid forest habitats of these ultramafic regions. Each of these genera belong to a separate evolutionary group (Smith *et al.* 2007) within a primarily endemic New Caledonian skink radiation as defined by the genetic data (Smith *et al.* 2007, Chapple *et al.* 2009), evidence the forces driving speciation in taxa with specialized biologies dependent on humid environments has impacted broadly across the skink fauna. The pattern of narrow-range endemism for these genera is comparable to the model of allopatric speciation associated with niche conservatism proposed by Wiens (2004) in which natural selection favours traits that keep individuals within the preferred niche and species fail to adapt to new conditions during vicariant events. It is such a scenario that has likely resulted in the evolution of a number of morphologically similar, yet genetically distinct, species in the genus *Sigaloseps* that are restricted to relictual forests near the summits of massifs, and as previously highlighted for *Marmorosphax* by Sadlier *et al.* (2009).

The genetic relationships between the species of *Sigaloseps* indicate patterns of broad scale regional vicariance across the southern region early in the history of the group, with subsequent deep and recent historical isolation of massifs giving rise to the evolution of the narrow-range, high-elevation endemic species seen within the '*ruficauda* group'. The low level of genetic divergence between the populations of *S. ferrugicauda* on Mt Ouin/Dzumac and the Humboldt massif indicate some degree of historical connectivity between these sites, and by inference connectivity of the high-elevation forest habitat. The morphological similarity of the population of *S. ferrugicauda* on the Kouakoué massif (albeit a single individual) with individuals from the Mt Ouin/Dzumac and Humboldt massifs indicates this connectivity of forest at high elevation probably extended to the Kouakoué massif, although this inference would benefit greatly from genetic data for the population on the Kouakoué massif. Conversely, the high level of genetic divergence between *S. ferrugicauda* and *S. ruficauda* would indicate a long-term isolation of the two taxa and the low level of morphological differentiation speciation by isolation consistent with niche conservatism model outlined above, inferring Mt Mou was isolated historically by contraction of preferred habitat (forest). However, the extremely low level of genetic differentiation between *S. ruficauda* and *S. balios*, and the distribution of these two species implies recent connectivity of preferred habitat (forest) across the ranges connecting these two sites. The apparent absence of *S. balios* (or a near relative) from the intervening ranges (Mt Ouin/Dzumac) between itself on Mt Humboldt and its sister taxon *S. ruficauda* on Mt Mou is difficult to explain, particularly given the inference from the genetic data for a level of recent historical connectivity between populations of *S. ferrugicauda* on Mt Humboldt and the Ouin/Dzumac range. *Sigaloseps balios* has only been recorded from habitat above 1300 m on Mt Humboldt. One possibility is that it was once more widespread along the high-elevation ridges in the region during cooler and moister climatic conditions but is now restricted to a higher elevational envelope (more so than other members of the '*ruficauda* group') accounting for its absence from the area investigated between 900-1100 m elevation on the Mt Ouin/Dzumac range.

Pintaud (2001) hypothesized the southern massif as one of four areas that would have sufficiently high rainfall to support rainforest refuges during periods of Pleistocene aridity, and as such it is possible these areas also acted as moist refugia during periods of aridity deeper in the past. The relatively deep split in the '*ruficauda* group' between *S. ferrugicauda* and (*S. ruficauda* + *S. balios*) would support evolution of two lineages via niche conservatism where the ancestral taxon was forced to high elevation areas on the ranges, with the lineage on Mt Mou becoming isolated and genetically divergent from populations on the interior ranges. The low genetic and morphological diversification seen within *S. ferrugicauda* would appear to support a pattern of relative stability between the constituent populations along the high-elevation interior ranges connecting Mt Humboldt, Ouin/Dzumac and Kouakoué, and by inference a long-term stability in the forest habitat at high elevation in these interior ranges. The extremely shallow level of genetic divergence

between *S. balios* and *S. ruficauda* and the apparently anomalous distribution of these sister taxa indicates that forest habitat in these ranges has both expanded and contracted significantly in more recent times, consistent with inferences made by Pintaud (2001) that historical distribution patterns have been blurred by Pleistocene climatic fluctuations and resulted in the present day patterns of distribution.

ACKNOWLEDGMENTS

The specimens used in this research project have been collected over a long period time under a number of permits and we thank the authorities of Province Nord and Province Sud for permission to conduct our herpetological research, and in particular the following individuals for their assistance with our research: Jean-Jérôme Cassan, Direction du Développement Économique et de l'Environnement (DDE-E), Province Nord; Anne-Claire Goarant (former Chef du service des milieux terrestres, Direction de l'environnement de la province Sud); and Joseph Manauté, Directeur Parc Provincial de la Rivière Bleue, Direction de l'environnement de la province Sud. Some of the samples used in this research were collected during the course of field surveys of mining leases and we gratefully acknowledge the assistance of staff of Société Le Nickel (SLN) and Vale-Nouvelle Calédonie for access to sites under their control and in certain instances commissioning the fieldwork. IRD Nouméa provided important logistical backing for our research in New Caledonia; Vivienne Whitaker, Cecilie Beatson, Glenn Shea and Marieke Lettink collaborated in field work. Michael Elliot of the Collection Informatics Unit, Australian Museum produced the map of distribution (figure 3). Ivan Ineich of the Muséum national d'Histoire naturelle provided the French résumé. This research was supported by grant DEB 0108108 from the National Science Foundation (U.S.A.) to A. M. Bauer and T. Jackman and by the project BIONEOCAL funded by the Agence Nationale de la Recherche (P. Grandcolas).

REFERENCES

- BAUER A.M. & SADLIER R.A. 2000 — *The Herpetofauna of New Caledonia*. (Society for the Study of Amphibians and Reptiles: Ithaca NY). 310 p., 24 pls.
- BAUER A.M. & SADLIER R.A. 1993 — Systematics, biogeography and conservation of the lizards of New Caledonia. *Biodiversity Letters* 1:107-122.
- BAUER A.M., JACKMAN T., SADLIER R.A., SHEA G. & WHITAKER A.H. 2008 — A new small-bodied species of *Bavayia* (Reptilia: Squamata: Diplodactylidae) from southeastern New Caledonia. *Pacific Science* 62(2): 247-256.
- BAUER A.M., JACKMAN T., SADLIER R.A. & WHITAKER A.H. 2006 — A Revision of the *Bavayia validiclavis* group (Squamata: Gekkota), a clade of New Caledonian Geckos Exhibiting Microendemism. *Proceedings of the California Academy of Sciences* 57(18): 503-547.
- BAUER A. M., SADLIER R.A., JACKMAN T.R. & SHEA G.S. 2012 — A new member of the *Bavayia cyclura* species group (Reptilia: Squamata: Diplodactylidae) from the southern ranges of New Caledonia. *Pacific Science* 66(2): 239-247.
- BAVAY A. 1869. — Catalogue des reptiles de la Nouvelle-Calédonie et description d'espèces nouvelles. *Mémoires de la Société Linnéenne de Normandie* 15:1-37.
- BOULENGER G.A. 1887 — *Catalogue of the Lizards in the British Museum (Natural History)*, Second Edition. Vol.3. British Museum (Natural History), London.
- BRENCHLEY J.L. 1873 — *Jottings during the Cruise of H.M.S. Curaçoa among the South Sea Islands in 1865*. Longmans, Green, and Co., London. xxviii + 487 p., 52 pls, 1 map.
- BRYGOO E.R. 1985 — Les types de Scincidés (Reptiles, Sauriens) du Muséum national d'Histoire naturelle. *Zoologie, Biologie et Écologie animales* 7(3): 1-126.
- CHAPPLE D.G., RITCHIE P.A. & DAUGHERTY C.H. 2009 — Origin, Diversification and Systematics of the New Zealand Skink Fauna (Reptilia: Scincidae). *Molecular Phylogenetics and Evolution* 52:470-487.
- RICHER DE FORGES B. & PASCAL M. 2008 — La Nouvelle-Calédonie, un point chaud de la biodiversité mondiale gravement menacé par l'exploitation minière. *Journal de la Société des Océanistes*: 126-127.
- DRUMMOND A.J. & RAMBAUT A. 2006 — BEAST v1.4. http://beast.bio.ed.ac.uk/Main_Page.
- DRUMMOND A.J., ASHTON B., BUXTON S., CHEUNG M., COOPER A., DURAN C., FIELD M., HELED J., KEARSE M., MARKOWITZ S., MOIR R., STONES-HAVAS S., STURROCK S., THIERERT. & WILSON A. 2011 — Geneious v5.4, available from <http://www.geneious.com/>
- FELSENSTEIN J. 1985 — Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39:783-791.
- HUELSENBECK J. & RONQUIST F. 2001 — MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17:754-755.
- JAFFRÉ T., MORAT P., VEILLON J.-M. & MACKEE H.S. 1987. — Changements dans la végétation de la Nouvelle-Calédonie au cours du Tertiaire: la végétation et la flore des roches ultrabasiqes. *Bulletin Muséum national d'Histoire naturelle, Paris* 4(9) section B, *Adansonia* 4: 365-391.
- MACEY J. J., LARSON A., ANANJEVA N. B., FANG Z. & PAPENFUSS T. J. 1997 — Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution* 14:91-104.

- MADDISON D. R. & MADDISON W. P. 2005 — MacClade: Analysis of Phylogeny and Character Evolution. v4.08. Sinauer Associates, Sunderland, Massachusetts.
- NYLANDER J. A. A., WILGENBUSCH J. C. WARREN D. L. & SWOFFORD D. L. 2008 — AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics* 24:581-583.
- PASCAL M., De FORGES B.R., Le GUYADER H. & SIMBERLOFFS D. 2008 — Mining and other threats to the New Caledonia Biodiversity Hotspot. *Conservation Biology* 22(2): 498-499.
- PINTAUD J.-C., JAFFRÉ, & PUIG, H. 2001 — Chorology of New Caledonian palms and possible evidence of Pleistocene rain forest refugia. *Comptes Rendus de l'Académie des Sciences Paris, Sciences de la vie / Life Sciences* 324:453-463.
- POSADA D. & CRANDALL K.A. 1998 — Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817-818.
- RONQUIST F. & HUELSENBECK J.P. 2003 — MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572-1574.
- ROUX J. 1913 — Les reptiles de la Nouvelle-Calédonie et des Îles Loyalty: 79-160 in Sarasin, F. & Roux, J. (eds.), Nova Caledonia, Zoologie, Vol. 1(2). C.W. Kreidels Verlag, Wiesbaden.
- SADLER R.A. 1986. — A review of the scincid lizards of New Caledonia. *Records of the Australian Museum* 39(1): 1-66.
- SADLER R.A. 2010 — Systematic studies of the scincid lizards of New Caledonia. PhD. Thesis, Griffith University, Queensland. 199 p.
- SADLER R.A. & BAUER A.M. 1999 — The scincid lizard genus *Sigaloseps* (Reptilia: Scincidae) from New Caledonia in the southwest Pacific: description of a new species and review of the biology, distribution, and morphology of *Sigaloseps deplanchei* (Bavay). *Records of the Australian Museum* 51(1): 83-91.
- SADLER R.A., BAUER A.M., WHITAKER A.H. & SMITH S.A. 2004a — Two New Species of Scincid Lizards (Squamata) from the Massif de Kopéto, New Caledonia. *Proceedings of the California Academy of Sciences* 55:208-221.
- SADLER R.A., SMITH S.A., BAUER A.M. & WHITAKER A.H. 2004b — A new genus and species of live-bearing scincid lizard (Reptilia: Scincidae) from New Caledonia. *Journal of Herpetology* 38(3): 320-330.
- SADLER R.A., BAUER A.M. & SMITH S.A. 2006a — A new species of *Nannoscincus* Günther (Squamata: Scincidae) from high elevation forest in southern New Caledonia. *Records of the Australian Museum* 58: 29-36.
- SADLER R.A., SMITH S.A. & BAUER A.M. 2006b — A New Genus for the New Caledonian Scincid Lizard *Lygosoma euryotis* Werner 1909, and the Description of a New Species. *Records of the Australian Museum* 58:19-28.
- SADLER R. A., SMITH S. A., BAUER A. M. & WHITAKER A. H. 2009 — Three new species of skink in the genus *Marmorosphax* Sadler (Squamata: Scincidae) from New Caledonia, in Grandcolas P. (ed.), Zoologia Neocaledonica 7. Biodiversity studies in New Caledonia. *Mémoires du Muséum national d'Histoire naturelle* 198: 373-390. Paris.
- SMITH S.A., SADLER R.A. & BAUER A.M., AUSTIN C.C. & JACKMAN T. 2007 — Molecular phylogeny of the scincid lizards of New Caledonia and adjacent areas: Evidence for a Single Origin of the endemic skinks of Tasmantis. *Molecular Phylogenetics and Evolution* 43: 1151-1166.
- STAMATAKIS A., HOOVER P. & ROUGEMONT J. 2008 — A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* 57:758-771.
- SWOFFORD D. L. 2002 — Paup Phylogenetic Analysis Using Parsimony (and Other Methods) Version 4.0. Sinauer Associates, Sunderland, Massachusetts.
- WHITAKER A.H. & SADLER R.A. 2011 — *Graciliscincus shonae*, in IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>. Downloaded on 28 November 2011.
- WIENS J.J. 2004 — Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution* 58(1):193-197.

APPENDIX 1

A list of specimens used in the genetic study. For museum acronyms see materials and methods.

GENUS	SPECIES	VOUCHER	LOCALITY	GENBANK ACCESSION
Outgroup				ND2
<i>Celatiscincus</i>	<i>euryotis</i>	AMS R.138574	île des Pins	DQ675204
<i>Graciliscincus</i>	<i>shonae</i>	AMS R. 165813	Mt. Ouin	DQ675207
<i>Kanakysaurus</i>	<i>viviparus</i>	AMS R.161299	île Pott, îles Belep	DQ675209
<i>Lacertoides</i>	<i>pardalis</i>	AMS R.148051	Kwa Néie	DQ675211
<i>Lioscincus</i>	<i>nigrofasciolatus</i>	AMS R.138624	île des Pins	DQ675216
<i>Lioscincus</i>	<i>steindachneri</i>	AMS R.149890	Mé Adéo	DQ675218
<i>Lioscincus</i>	<i>tillieri</i>	AMS R.148037	Mt. Vulcain	DQ675220
<i>Marmorosphax</i>	<i>tricolor</i>	CAS 214451	Mt. Koghis	DQ675227
<i>Phoboscincus</i>	<i>garnieri</i>	AMS R.151964	Mt. Dore	DQ675237
<i>Simiscincus</i>	<i>aurantiacus</i>	AMS R.144356	Mt. Koghis	DQ675250
<i>Tropidoscincus</i>	<i>variabilis</i>	AMS R.161879	Monts Kwa Né Mwa	DQ675242
Ingroup				
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172579	Port Boisé	KC164579
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.148065	Plaine des Lacs	DQ675238
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172580	Port Boisé	KC164580
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172581	Port Boisé	KC164581
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172587	Port Boisé	KC164582
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172605	Riv. des Pirogues (2)	KC164583
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172606	Riv. des Pirogues (2)	KC164584
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172607	Riv. des Pirogues (2)	KC164585
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172645	Yaté Barrage	KC164586
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172646	Yaté Barrage	KC164587
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172647	Yaté Barrage	KC164588
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.164353	Yaté	KC164589
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.164352	Yaté	KC164590
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.164242	Yaté	KC164591
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.168087	Plum	KC164592
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.168088	Plum	KC164593
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.168110	Riv. des Pirogues (1)	KC164594
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.168111	Riv. des Pirogues (1)	KC164595
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.168112	Riv. des Pirogues (1)	KC164596
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.168156	Rivière Blanche	KC164597
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.168157	Rivière Blanche	KC164598
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.147954	Rivière Blanche	KC164599
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172082	Kwé Nord	KC164600
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172083	Kwé Nord	KC164601
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.172084	Kwé Nord	KC164602
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.148064	Forêt Nord	KC164603
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.148065	Forêt Nord	DQ675238
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.164290	Pic du Pin	KC164604
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.164291	Pic du Pin	KC164605

<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.164257	Pic du Pin	KC164606
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.164258	Pic du Pin	KC164607
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.161884	Kwa Né Mwa	KC164608
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.167409	Ka Yé Wagwé	KC164609
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.167410	Ka Yé Wagwé	KC164610
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.167446	Forêt Cachée	KC164611
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.167447	Forêt Cachée	KC164612
<i>Sigaloseps</i>	<i>deplanchei</i>	AMB 6613	Mt Koghis	KC164613
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.135167	Yahoué	KC164614
<i>Sigaloseps</i>	<i>conditus</i> n. sp.	AMS R.171426	Pourina River	KC164615
<i>Sigaloseps</i>	<i>conditus</i> n. sp.	AMS R.147916	Rivière Bleue	KC164616
<i>Sigaloseps</i>	<i>conditus</i> n. sp.	AMS R.147952	Rivière Bleue	KC164617
<i>Sigaloseps</i>	<i>conditus</i> n. sp.	AMS R.147953	Rivière Bleue	KC164618
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R. 172503	Nakéty	KC164619
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R. 172504	Nakéty	KC164620
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R. 172505	Nakéty	KC164621
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R. 172507	Nakéty	KC164622
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R. 172512	Nakéty	KC164623
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R. 172513	Nakéty	KC164624
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R. 172514	Nakéty	KC164625
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R.171249	Pic Ningua	KC164626
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R.171250	Pic Ningua	KC164627
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R.171254	Pic Ningua	KC164628
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R.171255	Pic Ningua	KC164629
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R.172555	Tontouta valley	KC164630
<i>Sigaloseps</i>	<i>pisinnus</i> n. sp.	AMS R.172576	Tontouta valley	KC164631
<i>Sigaloseps</i>	<i>ruficauda</i>	AMS R.146482	Mt Mou	DQ675239
<i>Sigaloseps</i>	<i>ruficauda</i>	AMS R.148004	Mt Mou	KC164632
<i>Sigaloseps</i>	<i>ferrugicauda</i> n. sp.	AMS R.172611	Mt Humbolt	KC164633
<i>Sigaloseps</i>	<i>ferrugicauda</i> n. sp.	AMS R.162964	Mt Ouin	KC164634
<i>Sigaloseps</i>	<i>balios</i> n. sp.	AMS R.172620	Mt Humboldt	KC164635
<i>Sigaloseps</i>	<i>balios</i> n. sp.	AMS R.172621	Mt Humboldt	KC164636
<i>Sigaloseps</i>	<i>balios</i> n. sp.	AMS R.172623	Mt Humboldt	KC164637

High elevation endemism on New Caledonia's ultramafic peaks – a new genus and two new species of scincid lizard

Ross A. Sadlier ⁽¹⁾, Aaron M. Bauer ⁽²⁾, Sarah A. Smith ⁽³⁾, Glenn M. Shea ⁽⁴⁾ & [†]Anthony H. Whitaker ^(5, 6)

⁽¹⁾ Section of Herpetology, Australian Museum, 6 College Street, Sydney 2000, NSW, Australia
rosss@austmus.gov.au

⁽²⁾ Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA

⁽³⁾ Eco Logical Australia Pty Ltd., 16/56 Marina Boulevard Cullen Bay 0820, NT, Australia

⁽⁴⁾ Faculty of Veterinary Science B01, University of Sydney, NSW 2006, Australia

⁽⁵⁾ Whitaker Consultants Limited, 270 Thorpe-Orinoco Road, Orinoco, RD1, Motueka 7196, New Zealand

ABSTRACT

Field research on the ultramafic ranges of New Caledonia has resulted in the discovery of two new species of scincid lizard, each only known from a single mountain. One is from the summit of Mt Taom in the northwest, the other from near the summit of Mt Ouin in the southern region. Genetic data for the species from Mt Taom indicates that it is related to a broader group of taxa that includes *Caledoniscincus*, *Simiscincus* and *Graciliscincus*, but is not congeneric with any of these. It is superficially similar in morphology to species in the genus *Caledoniscincus*, but lacks the full suite of diagnostic apomorphies of that genus. As such, it is accorded generic rank on the basis of genetic criteria supported by a suite of morphological apomorphies unique within the *Eugongylus* group of skinks. The new species from Mt Ouin does not have genetic data to support its generic placement. However, it has a limited suite of morphological apomorphies that are more consistent with allocation to the new genus proposed here than to any existing genus of New Caledonian skink, and therefore its placement is as much by default rather than a statement of close relationship.

The restricted distribution of both species to areas that are either under threat, or potentially threatened by mining activities, identifies them as being at a high level of risk when assessed on IUCN criteria for allocation to category of threat.

RÉSUMÉ

Endémisme de haute altitude sur les pics ultramafiques de Nouvelle-Calédonie - un nouveau genre et deux nouvelles espèces de lézards scincides.

Les recherches de terrain sur les massifs ultramafiques de Nouvelle-Calédonie ont permis la découverte de deux nouvelles espèces de scinques, connues chacune respectivement d'une seule montagne. L'une provient du sommet du Mt Taom dans le nord-ouest, l'autre de la proximité du sommet du Mt Ouin dans la région sud. Les données obtenues sur la génétique de l'espèce du Mt Taom indiquent des liens avec un groupe plus large de taxons comprenant *Caledoniscincus*, *Simiscincus* et *Graciliscincus*, mais elle n'est congénérique d'aucun d'entre eux. Elle est superficiellement semblable, morphologiquement, à des espèces du genre *Caledoniscincus*, mais ne présente pas la série de caractères apomorphes caractéristiques de ce genre. Nous lui accordons par conséquent un rang générique sur la base de critères génétiques, appuyés par une série d'apomorphies morphologiques uniques chez les scincides du groupe *Eugongylus*. La nouvelle espèce du Mt Ouin ne présente pas de caractères génétiques propres permettant de justifier son placement dans un genre particulier, mais présente une série limitée d'apomorphies morphologiques qui sont plus en accord avec son inclusion dans le nouveau genre décrit ici, plutôt que dans aucun autre genre actuellement reconnu chez les scincides de Nouvelle-Calédonie. Son attribution générique est donc opérée par défaut plutôt que sur la base de réelles affinités. La répartition restreinte des deux espèces dans des zones soit menacées, soit potentiellement menacées par les activités minières, nous oblige à les ranger, selon les critères définis par l'UICN, dans une catégorie gravement menacée.

INTRODUCTION

Ultramafic substrates formed below the sea and brought to the surface by the overthrust of the underlying continental plate during the Pliocene gave rise to the ultrabasic soils which cover a large part of the New Caledonian landscape. Ultramafic substrates now occur on the island as an extensive block in the southern region, a series of ranges in south of the central-east region, and as an extensive chain of often isolated near-coastal massifs in the central-west and north-west regions (Éditions du Cagou 1992). The soils have exceptionally high levels of iron and magnesium, and several heavy metals, most notably nickel, a feature considered as having had a significant effect on the evolution and diversification of New Caledonia's vegetation (Lowry 1998; Pintaud *et al.* 2001a). They are also the basis for the mainstay of the territory's economy, nickel mining.

The ultramafic block in the southern region is a complex of steep ranges and deep river valleys that extends across most of southern Grande Terre north to the Thio valley. In this region ranges on the drier west side are now dominated by maquis shrubland with humid forest patches in the upper reaches of the river valleys and near the summits of the ranges. More continuous areas of humid forest occur on the aggregation of high-elevation ranges that link the Massif du Kouakoué, Mt Dzumac and Massif du Humbolt. This group of ranges receives a very high rainfall, generally above 3000 mm/year, a trait identified as a key factor in their likely role as moist refugia in historical periods of climatic aridity (Pintaud 2001b). By contrast the isolated massifs that make up the near-coastal ultramafic ranges of the central-west and north-west regions are typically dominated maquis shrubland with patches of humid forest, generally only near the summit, and rainfall in these mountains is now typically low and highly seasonal.

Our studies have identified the ultramafic ranges of the southern region and the west-central/north-west ultramafic region as distinctive biogeographic zones for lizards, with each having a rich and uniquely endemic fauna. In particular our investigations have revealed the existence of a number of narrow-range, massif-specific taxa in the northwest region. The level of localised endemism in this region, which includes a number of taxa that are moisture-sensitive and restricted to high elevation, is testament to the long-term persistence (and isolation) of suitable habitat on the summits of these mountains during periods of historical dryness. The evolutionary scenario for lizards in the southern ultramafic ranges is more complex in that there is evidence for both narrow-range (altitude dependent) endemism (*Marmorosphax* – Sadlier *et al.* 2009) and broader scale (altitude independent) localized endemism (*Bavayia* – Bauer *et al.* 2012) within the region, indicating the potential for speciation driven by cladogenic factors other than historical isolation on mountain summits.

The new species described here are each known only from a single high-elevation site on ultramafic surfaces and both are known only from a single individual, despite repeated visits to the original collection sites and survey work in

adjacent areas. It is highly likely they each represent yet another example of extreme high-elevation microendemism that characterises the ultramafic ranges of these regions.

Ironically these ultramafic regions, which hold a significant part of the territory's natural patrimony in terms of endemic biota, are also the regions in which a significant part of its mineral wealth resides, this conundrum has been highlighted by Jaffré (2005) in identifying forests and shrubby maquis on ultramafic rocks as being one of the vegetation types now most at risk in New Caledonia. Further exacerbating this situation is the fact that many species unique to these regions are only found near the summits of massifs, areas that have been or will be under the greatest pressure from mining activities. Concerns have been raised (Pascal *et al.* 2008) regarding the gaps in the knowledge of the natural environment in the face of escalating expansion of mining, and the impacts of these on decision-making regarding conservation of the territory's natural heritage. The uniqueness of the high-elevation plant communities and the significance of high-elevation habitats for the biodiversity of the New Caledonian flora has already been highlighted (Nasi *et al.* 2002; Jaffré *et al.* 2010), and a review of the conservation status of conifer species on ultramafic substrates (Jaffré *et al.* 2010) raised concerns regarding the relatively small proportion of high-elevation (above 900 m) areas that are protected and the importance of not allowing mine exploration within these reserves. Our own investigations have led to the recognition an extensive number of lizard species endemic to ultramafic surfaces with distributions restricted to habitats above 900m in elevation, not only adding further support to the uniqueness of this environment for fauna but also the significant role played by the summit areas of these massifs in the evolution of the island's faunal diversity (Sadlier *et al.* 2004; Sadlier *et al.* 2006; Sadlier *et al.* 2009).

The summit areas of many ultramafic peaks have not been surveyed or have only received preliminary investigation for lizards, particularly in the southern region, and the current state of knowledge is likely to represent a significant underestimation of the extent of high-elevation endemism in the lizard fauna. These ultramafic regions of New Caledonia, particularly the high-elevation habitats, are now likely to be the areas of greatest conservation significance and concern for lizards on Grande Terre, and are also likely to be of equal or greater significance for the conservation of the territory's still largely undocumented terrestrial invertebrate fauna.

MATERIALS AND METHODS

Specimen numbers are prefixed as follows: MNHN: Muséum national d'Histoire naturelle, Paris; AMS: Australian Museum, Sydney.

The following suite of morphological characters was scored for the type (and only known) specimen of each species: snout to vent length (SVL) - measured from tip of snout to caudal edge of anal scales; axilla to groin distance - measured from middle of base of forelimb to base of hindlimb; forelimb to snout length - measured from tip of snout to middle of base of forelimb; hindlimb length - measured from middle of base of hindlimb to tip of fourth toe including nail; tail length - measured from caudal edge of anal scales to tip of tail, the degree to which the original tail is present being determined by X-ray. Body measurements are also expressed as a percentage of snout to vent length.

Head scalation generally follows Taylor (1935) as described and figured by Sadlier (1986); midbody scale rows—number of longitudinal scale rows around body counted midway between axilla and groin; paravertebral scales—number of scales in a paravertebral row from first scale posterior of parietal scale to last scale at level of vent opening; fourth finger and toe scales—number of dorsal scales on fourth digit of hand and foot (distal scale contains claw; basal scale of fourth finger is usually present as a single large scale common to the base of the fourth, third, and second finger; basal scale of fourth toe broadly contacts basal scale of adjacent third toe; fourth finger); and toe lamellae—number of ventral scales on fourth digit of hand and foot, distal scale contains claw and basal scale is last largely undivided scale at a point level with intersection of third and fourth digits. Bilateral scalation characters were scored on both sides and the mean value used.

Phalangeal formula and the number of presacral vertebrae were assessed by X-ray.

Character polarities follow Sadlier (2010).

The content and order of authors for the description of each species reflects the individual contributions of those individuals to the discovery and recognition of that species, and as such does not necessarily reflect the content and arrangement of authors for this article as a whole.

SYSTEMATIC PART

The two species in the new genus proposed here are superficially very similar to species in the genus *Caledoniscincus*. Genetic data (Smith *et al.* 2007) provides a broad-scale comparison between the new genus (as represented by the type species – the individual from Mt Taom) and the majority of other New Caledonian skinks, and clearly identifies it as belonging to a lineage that includes *Caledoniscincus*, *Simiscincus* and *Graciliscincus*, but which is as divergent from these genera as they are from each other. This arrangement receives some (limited) support (Sadlier 2010) from a suite of morphological apomorphies unique within the *Eugongylus* group of skinks as defined by Greer (1979) that would recognise it as the sister to, but not congeneric with, *Caledoniscincus*.

Family SCINCIDAE Gray, 1825

Genus **PHAEOSCINCUS** Sadlier, Smith, & Bauer, n. gen.

Type species. *Phaeoscincus toamensis* Sadlier, Whitaker, Smith & Bauer, n. sp.

DIAGNOSIS — *Phaeoscincus* is a member of the *Eugongylus* group of skinks as defined by Greer (1979), it can be distinguished from all genera in that group by the following combination of character states for body proportions, scalation and osteology (apomorphic character states with the concept of the *Eugongylus* group of skinks denoted by an asterisk* - polarities defined in Sadlier 2010).

Body proportions. Moderately small in size (range of maximum snout vent lengths for included species 38–40 mm) with moderately elongate body, well developed limbs and digits, and moderately long tail (~150% of SVL).

Scalation. Naris situated within a single undivided nasal scale; frontonasal broader than long; prefrontals reduced in size and widely separated; frontal nearly as broad as long; supraoculars four; frontoparietals paired; interparietal distinct; parietals in broad contact behind interparietal, and each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; lower secondary temporal single (*ouinensis* n. sp. – Mt Ouin) or divided* (*toamensis* n. sp. – Mt Taom) to form two equal sized scales bordering the posterior edge of the primary temporal between the last upper labial and upper secondary temporal scales; tertiary temporals two; postlabials two; nasals moderately to widely separated; anterior loreal reduced, higher than wide; supraciliaries 7; upper labials 7 with the fifth subocular and contacting the lower eyelid; lower labials 6; loreals two, anterior noticeably deeper than long, posterior as long as deep and shallower than anterior; postmental contacting first and second lower labial; transversely enlarged chinshields three, first pair in broad contact, second pair separated by one scale, third pair separated by three scales; *dorsal body scales with 3 strong keels dorsally; lower eyelid with an obvious, centrally-located, semi-transparent disc.

Osteology. Premaxillary teeth 11; presacral vertebrae 29; phalangeal formula for the manus 2.3.4.5.3 and for the pes 2.3.4.5.4.

COMMENTS — Two independent genetically-based studies (Smith *et al.* 2007; Chapple *et al.* 2009) have each identified the endemic New Caledonian skink genera as belonging to a radiation that also includes the endemic New Zealand skinks and the endemic Lord Howe Island/Norfolk Island species, and in one of these studies (Chapple *et al.* 2009) is the monophyletic sister to the New Zealand + Lord Howe Island/Norfolk Island taxa. No single morphological feature supports this scheme of relationships. The genetic phylogeny for the endemic New Caledonian skink genera (complimented



FIGURE 1

Holotype of *Phaeoscincus taomensis* (MNHN 2003.1005).

by an extensive sampling of *Eugongylus*-group taxa) published by Smith *et al.* (2007) included the type species of the new genus proposed here (as 'New Genus Mt Taom'), placing this taxon within a well supported New Caledonian lineage of endemic genera and as distinct from a monophyletic *Caledoniscincus*.

Within the context of this lineage of endemic New Caledonian skink genera the suite of morphological apomorphies possessed by the species from Mt Taom clearly indicates it is not congeneric with any existing genus. In most aspects of morphology, *Phaeoscincus* gen. nov. most closely resembles the New Caledonian genus *Caledoniscincus*, but lacks a significant apomorphic state, fused frontoparietal scales, for inclusion in a monophyletic *Caledoniscincus* of thirteen species.

ETYMOLOGY — The name for the genus is derived from the Greek *phaios* brown and *skinkos* for skink, meaning 'brown skink' which describes the overall 'non-descript' appearance of the members of the genus.

***Phaeoscincus taomensis* Sadlier** Whitaker, Smith & Bauer, n. sp.

Figures 1-3

TYPE MATERIAL — Holotype: New Caledonia, MNHN 2003.1005 (formerly AMS R.161182) Mt Taom, Massif d'Ouazan-gou-Taom, 20°47'04.8"S 164°34'42.3"E (elevation 1020 m.) collected by A.H. & V.A. Whitaker, 12 June 2002.

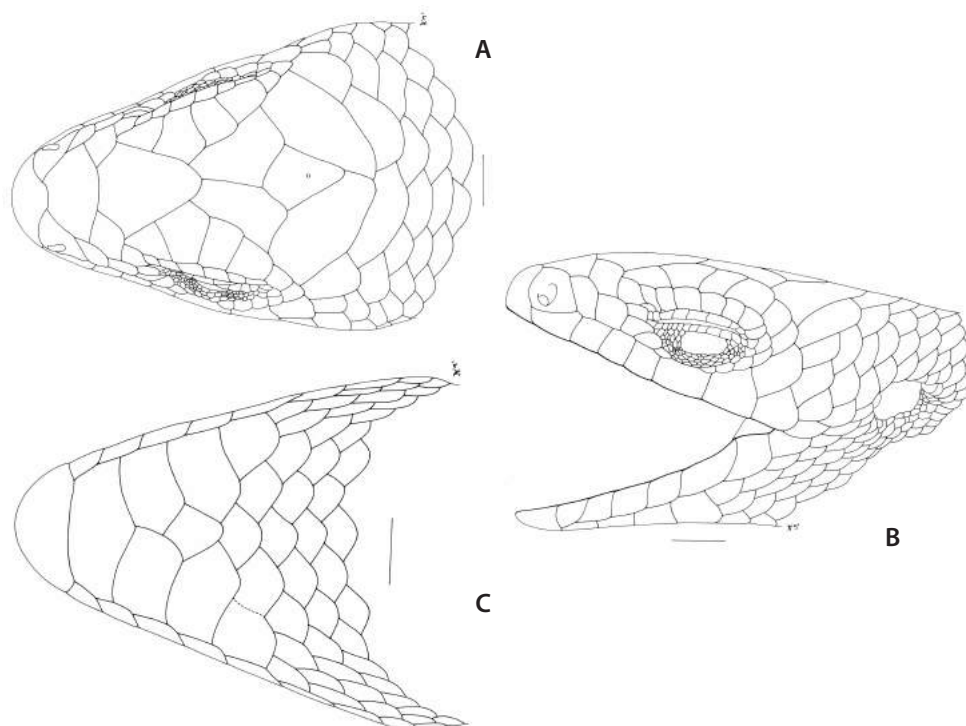


FIGURE 2
Dorsal (A), lateral (B), and ventral (C) views of the headshields of *Phaeoscincus taomensis* (MNHN 2003.1005).

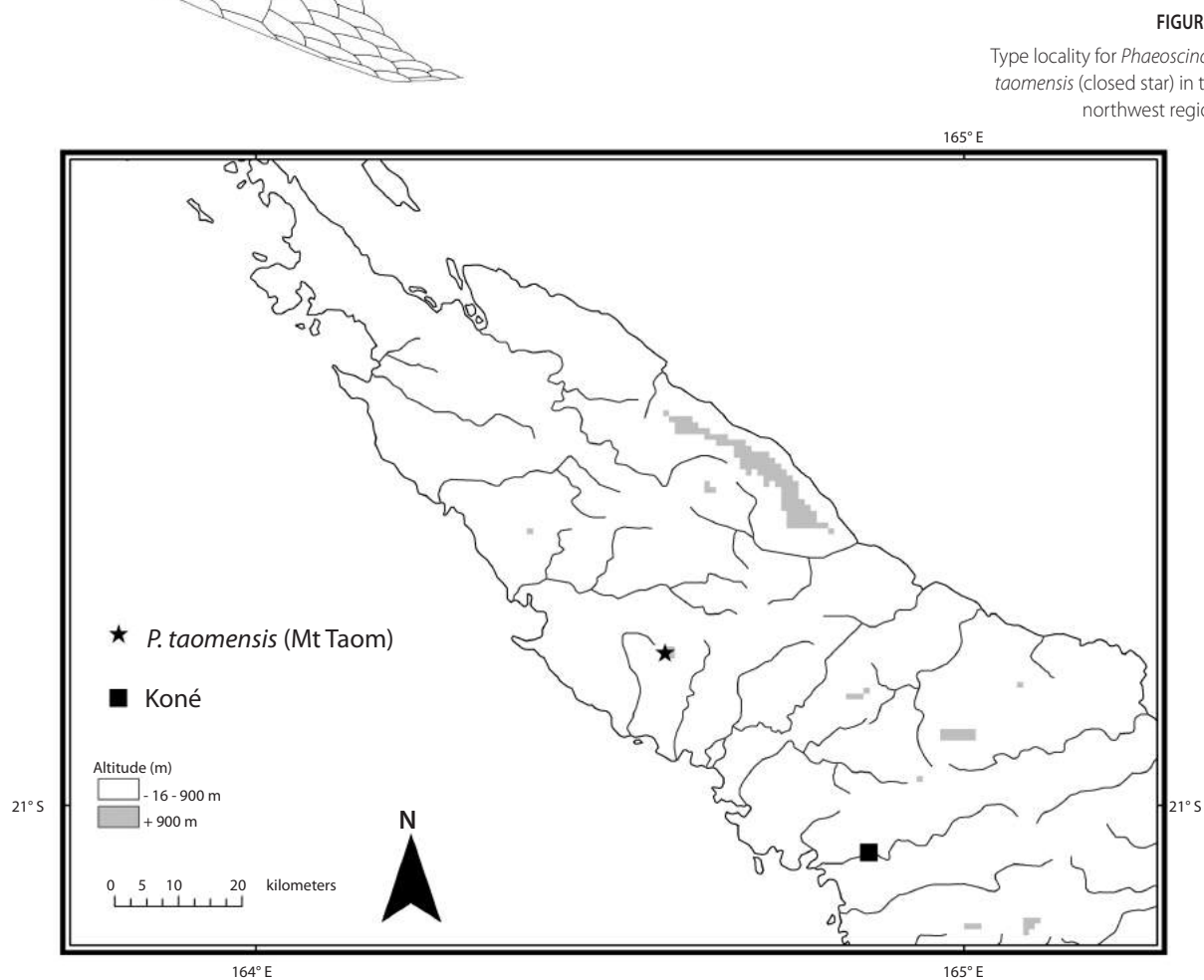


FIGURE 3
Type locality for *Phaeoscincus taomensis* (closed star) in the northwest region.

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

DIAGNOSIS — *Phaeoscincus taomensis* n. sp. can be distinguished from the only other member of the genus, *Phaeoscincus ouinensis* n. sp., in having two (vs single) lower secondary temporal scales, and significantly more lamellae beneath fourth finger (mean = 15 vs 12), scales on top of fourth toe (mean = 14.0 vs 11.5) and lamellae beneath fourth toe (mean = 29.5 vs 21.5).

DESCRIPTION — Based on the only known specimen, the holotype, a subadult male.

Measurements. SVL 38 mm; distance from axilla to groin 21 mm (55.3% of SVL); distance from forelimb to snout 15 mm (39.5% of SVL); hindlimb length 13 mm (34.2% of SVL); tail length 46.0 mm, reproduced.

Scalation. midbody scale rows 28; paravertebral scales 62; scales on top of fourth finger 9-10 (mean = 9.5); lamellae beneath fourth finger 15-15 (mean = 15); scales on top of fourth toe 14-14 (mean = 14.0); lamellae beneath fourth toe 29-30 (mean = 29.5).

Osteology. Presacral vertebrae 29; phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4 respectively.

Coloration. Dorsal surface of body mid-brown overall, each scale with a dark marking medially of varying intensity to give the appearance of numerous fine dark flecks. Lateral surface of body dark brown to blackish uppermost, becoming lighter approaching the venter and with a paler centre to each scale giving a speckled appearance. Head scales mid-brown with a reddish tinge in life, supraocular scales with a dark edging posteriorly, and the rostral scale without obvious dark marking medially. Ventral surface grey with a dark brown blotch to the posterior edge of each scale of the chest, abdomen and tail giving a spotted appearance.



FIGURE 4

Summit of Mt Taom showing remnant patches of closed forest (A) and widespread maquis habitat (B) on a cuirasse cap.

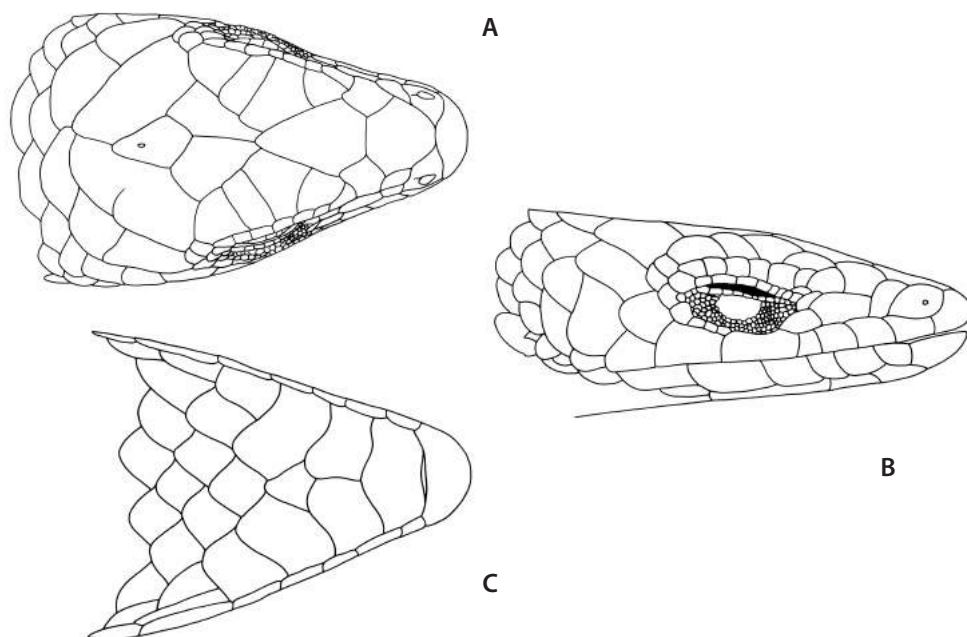


FIGURE 5

Dorsal (A), lateral (B), and ventral (C) views of the headshields of *Phaeoscincus ouinensis* (MNHN 2011.0276).

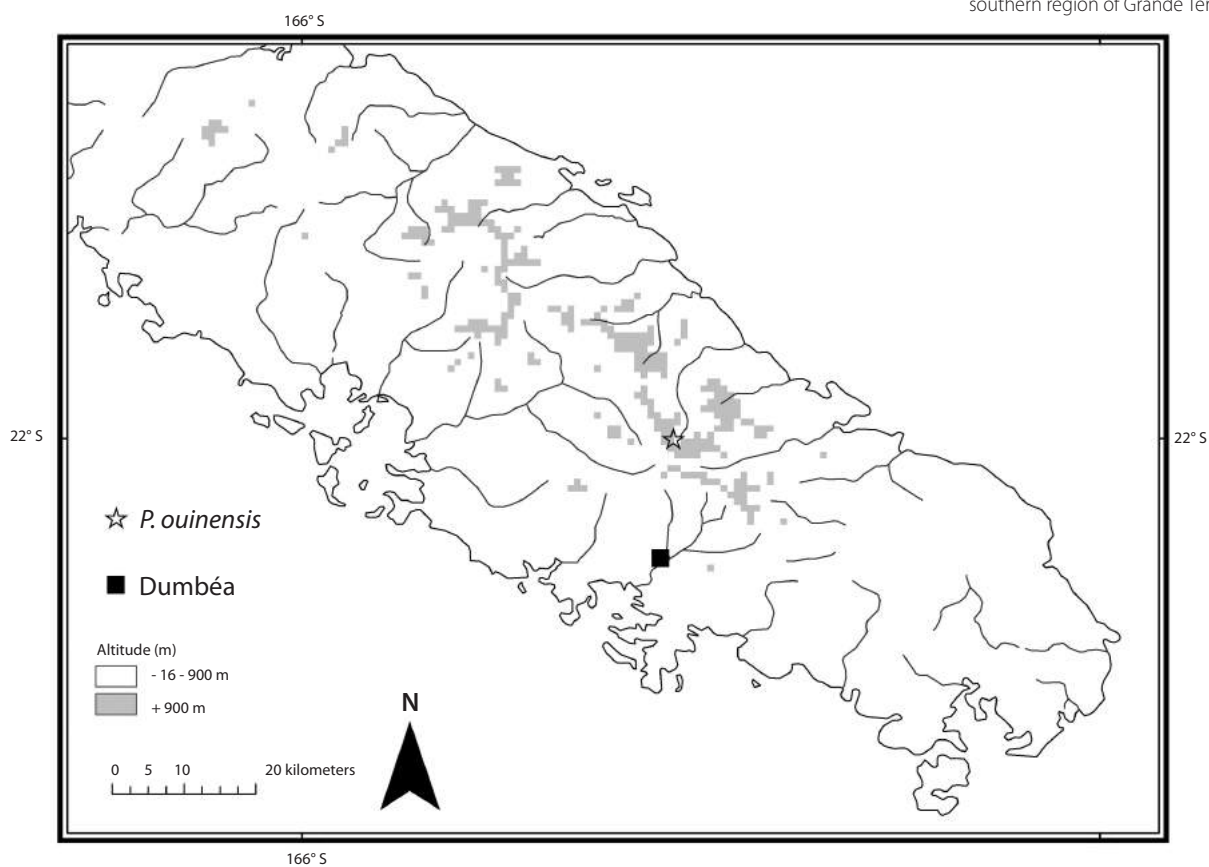


FIGURE 6

Type locality for *Phaeoscincus ouinensis* (open star) in the southern region of Grande Terre.

DISTRIBUTION AND HABITAT — Mt Taom is located in the northwest of the island (Figure 2) close to the coast about 40 km north of the town of Koné. The mountain is covered with maquis shrubland and has small patches of closed forest on the slopes and at the summit (Figure 4). The holotype was collected in high-elevation maquis shrubland with a thick groundcover of the fern *Gleichenia* sp. on a broken lateritic cuirasse surface.

COMPARISON WITH OTHER SPECIES — *Phaeoscincus taomensis* n. sp. most closely resembles subadult male and adult female *Caledoniscincus atropunctatus* from the north-western region ultramafic ranges. It is readily distinguished from this species by differences in head scalation in having divided (vs fused) frontoparietal scales and two (vs single) lower secondary temporals.

Phaeoscincus ouinensis Sadlier, Shea & Bauer, n. sp.

Figures 5-7

TYPE MATERIAL — Holotype: New Caledonia, MNHN 2011.0276 (formerly AMS R.165819) Mt Ouin, track along northeast edge of Mt Ouin Range, 22°00'S 166°28'E (elevation ~1000 m), collected by R.A. Sadlier and G.M. Shea, 27 December 2003.

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

DIAGNOSIS — See above under diagnosis for *Phaeoscincus taomensis* n. sp.

DESCRIPTION — Based on the only known specimen, the holotype, a reproductively mature adult female with 1/2 large yolked ovarian follicles and a convoluted oviduct; SVL 39.5 mm; distance from axilla to groin 22 mm (55.7% of SVL; distance from forelimb to snout 14.5 mm (36.7% of SVL); hindlimb length 14.0 mm 35.4% of SVL; tail length 47 mm, last 10 mm reproduced.

Scalation. Midbody scale rows 28; paravertebral scales 58; scales on top of fourth finger 9-9 (mean = 9); lamellae beneath fourth finger 12-12 (mean = 12); scales on top of fourth toe 11-12 (mean = 11.5); lamellae beneath fourth toe 20-21 (mean = 20.5).

Osteology. Presacral vertebrae 29; phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4 respectively.

Coloration. Body two-toned. Dorsal surface of body and head uniformly light-mid brown. Lateral surface of the body dark brown-black uppermost grading to mid-brown approaching the venter, side of neck and head dark brown-black. Rostral scale without obvious dark marking medially. Ventral surface pale and without any dark markings.

DISTRIBUTION AND HABITAT — Mt Ouin is located in the southern ultramafic region of Grande Terre (Figure 6) in the central ranges. The specimen was collected from a track at the edge of humid forest habitat at ~1000 m elevation (Figure 7).

COMPARISON WITH OTHER SPECIES — The single adult female *Phaeoscincus ouinensis* n. sp. most closely resembles subadult and adult female *Caledoniscincus austrocaledonicus* from the southern region ultramafic ranges, and with which it is sympatric. It is readily distinguished from regionally sympatric populations of this species by differences in head scalation in having divided (vs fused) frontoparietal scales and fewer lamellae scales of the fourth digit of the pes (20-21 vs 23-28). It also resembles subadult and adult female *Caledoniscincus notialis* with which it is sympatric, and like this species lacks a noticeable mid-rostral streak. It can be distinguished from regionally sympatric *C. notialis* in having divided (vs fused) frontoparietal scales and fewer lamellae scales of the fourth digit of the manus (12 vs 14-19) and pes (20-21 vs 26-35).

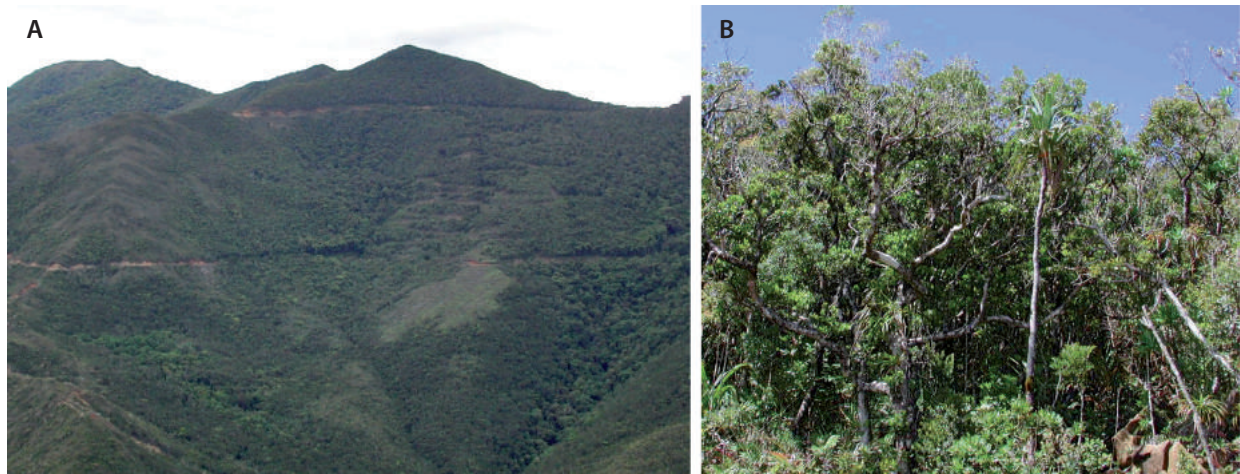


FIGURE 7

Mt Ouin in the southern ultramafic ranges - note closed forest habitat is largely restricted to gullies and summit of the range (A), where it is low and dense (B) with extensive outcropping of peridotite on the forest floor.

DISCUSSION

Our research indicates that a significant number of lizard species in New Caledonia are restricted to individual ultramafic peaks, some of these to high-elevation habitat. Because of their extremely restricted areas of occupancy, and the narrow environmental envelopes occupied, the conservation of these species present a special challenge, particularly given the past and potential future impacts from mining.

Phaeoscincus taomensis n. sp. is known from a single site on Mt Taom. The area of habitat >900 m elevation on the massif is estimated at <5 km². The greatest threat to *P. taomensis* n. sp. is loss of habitat leading to a reduction in the area of occupancy. The summit area of Mt Taom has a network old mining exploration tracks and there is intensive mining activity nearby at around 800 m. Given the small area of habitat >900 m on the massif and the threats to habitat on the summit area from fire and the expansion of mining activities, the species is assigned a category of Critically Endangered B1ab(i-iii,v) under IUCN criteria (IUCN 2001).

Phaeoscincus ouinensis n. sp. is known from a single site on the Mt Ouin/Dzumac range. The area of high-elevation forest >900 m on these ranges is estimated at about 25 km², probably more given the extent of the high-elevation forested area along the watershed connecting Mt Dzumac with Montagne des Sources. The greatest threat to *P. ouinensis* n. sp. is loss of habitat leading to a reduction in the area of occupancy. There is currently no mining development on the summit areas of Mt Ouin/Dzumac range other than the recent upgrading of the road that gives access to the Ni River valley. However, the proximity of mining activity in the nearby Tontouta Valley system and recent improvement in access to the Ni Valley increases the risk of peripheral damage and a reduction in the extent of montane forest in this region from wildfires in the adjacent maquis shrubland. Furthermore, introduced ungulates (deer and pigs) threaten habitat quality by damaging the litter layer. *Phaeoscincus ouinensis* n. sp. is conservatively categorized as Vulnerable (D2) under IUCN criteria on its extremely restricted distribution, but could be moved to a higher level of threat in face of an increased decline in area, extent and/or quality of habitat from introduced species or should mining activities intensify in the future.

ACKNOWLEDGMENTS

The authors thank the New Caledonian authorities for their support in providing permits to collect and conduct field research in New Caledonia, in particular Jean-Jérôme Cassan (Direction du Développement Économique et de l'Environnement (DDE-E), Province Nord) and Anne-Claire Goarant (former Chef du Service des Milieux Terrestres, Direction de l'Environnement (DENV), Province Sud). Special thanks are due to Joseph Manauté (DENV) for his support in initiating and funding the survey during which *P. taomensis* n. sp. was discovered. Logistical support in Nouméa was provided by Hervé Jourdan (Institut de Recherche pour le Développement (IRD), Nouméa); Vivienne Whitaker assisted with the survey of Mt Taom. Illustrations of head shields were produced by Hannah Finlay (Figure 3) and Cecilie Beatson (Figure 6), and the distribution map (Figure 1) was produced by Michael Elliot of the Collection Informatics Unit, Australian Museum. Ivan Ineich of the Muséum national d'Histoire Naturelle, Paris, provided the French resumé. We thank SMSP for permission to conduct research on the mining lease on Mt Taom.

REFERENCES

- BAUER A. M., SADLIER R. A., JACKMAN T. R. & SHEA G. S. 2012 — A new member of the *Bavayia cyclura* species group (Reptilia: Squamata: Diplodactylidae) from the southeast ranges of New Caledonia. *Pacific Science* 66(2): 239-247.
- CHAPPLED D. G., RITCHIE P. A. & DAUGHERTY C. H. 2009 — Origin, diversification and systematics of the New Zealand skink fauna (Reptilia: Scincidae). *Molecular Phylogenetics and Evolution* 52: 470-487.
- ÉDITIONS DU CAGOU 1992 — Atlas de Nouvelle Calédonie. Hachette Calédonie. 91 pp.
- GREER A. E. 1979. — A phylogenetic subdivision of Australian skinks. *Records of the Australian Museum* 32(8): 339-371.
- IUCN 2001 — 'IUCN Red List categories: Version 3.1'. IUCN Species Survival Commission, Gland, Switzerland, and Cambridge, UK. 26 p.
- JAFFRÉ T. 2005 — Conservation programmes in New Caledonia, western Pacific: in place for the dry forest, but urgently needed for ultramafic vegetation. *BG Journal* 2(1): 13.
- JAFFRÉ T., MUNZINGER J. & LOWRY P. P. II. 2010 — Threats to the conifer species found on New Caledonia's ultramafic massifs and proposals for urgently needed measures to improve their protection. *Biodiversity Conservation* 19: 1485-1502.
- LOWRY P. P. II. 1998 — Diversity, endemism, and extinction in the flora of New Caledonia: a review, in PENG C. J., LOWRY P. P., II (eds), Rare, threatened, and endangered floras of Asia and the Pacific Rim. Institute of Botany, *Academia Sinica Monograph Series Taipei* 16: 181-206.
- NASI R., JAFFRÉ T. & SARRAILH J.-M., 2002 — Les forêts de montagne de la Nouvelle-Calédonie. *Bois et Forêts des Tropiques* 274 (4): 5-18.
- PASCAL M., RICHER DE FORGES B., LE GUYADER H. & SIMBERLOFFS D. 2008. — Mining and other threats to the New Caledonia Biodiversity Hotspot. *Conservation Biology* 22(2): 498-499.
- PINTAUD J.-C. & JAFFRÉ T. 2001a — Patterns of diversity and endemism in palms on ultramafic rocks in New Caledonia. *South African Journal of Science* 97:548-550.
- PINTAUD J.-C., JAFFRÉ T. & PUIG H. 2001b — Chronology of New Caledonian palms and possible evidence of Pleistocene rain forest refugia. *Comptes Rendus de l'Académie des Sciences Paris, Sciences de la vie / Life Sciences* 324:453-463.
- SADLIER R. A. 1986 — A review of the scincid lizards of New Caledonia. *Records of the Australian Museum* 39(1): 1-66.
- SADLIER R. A. 2010 — Systematic studies of the scincid lizards of New Caledonia. PhD. Thesis, Griffith University, Queensland. 199 p.
- SADLIER R. A., BAUER A. M., WHITAKER A. H. & SMITH S. A. 2004 — Two new species of scincid lizards (Squamata) from the Massif de Kopeto, New Caledonia. *Proceedings of the California Academy of Sciences* 55(11): 208-221.
- SADLIER R. A., BAUER A. M. & SMITH S. A. 2006 — A new species of *Nannoscincus* Günther (Squamata: Scincidae) from high elevation forest in southern New Caledonia. *Records of the Australian Museum* 58: 29-36.
- SADLIER R. A., BAUER A. M., WOOD P. L., SMITH S. A., WHITAKER A. W., JOURDAN H. & JACKMAN T. 2014 — Localized endemism in the southern ultramafic bio-region of New Caledonia as evidenced by the scincid lizards in the genus *Sigaloseps* (Reptilia: Scincidae), with a description of four new species, in GUILBERT É., ROBILLARD T., JOURDAN H. & GRANDCOLAS P. (eds), *Zoologia Neocaledonica* 8. Biodiversity studies in New Caledonia. *Mémoires du Muséum national d'Histoire naturelle*, 206: 81-115.
- SADLIER R. A., SMITH S. A., BAUER A. M. & WHITAKER A. H. 2009 — Three new species of skink in the genus *Marmorosphax* Sadlier (Squamata: Scincidae) from New Caledonia, in Grandcolas P. (ed.), *Zoologia Neocaledonica* 7. Biodiversity studies in New Caledonia. *Mémoires du Muséum national d'Histoire naturelle* 198: 373-390.
- SMITH S. A., SADLIER R. A., & BAUER A. M., AUSTIN C. C. & JACKMAN T. 2007 — Molecular phylogeny of the scincid lizards of New Caledonia and adjacent areas: Evidence for a single origin of the endemic skinks of Tasmantis. *Molecular Phylogenetics and Evolution* 43: 1151-1166.
- TAYLOR E. H. 1935 — A taxonomic study of the cosmopolitan scincoid lizards of the genus *Eumeces* with an account of the distribution and relationships of its species. *Science Bulletin of the University of Kansas* 36 (14): 642.

New data on freshwater fishes of New Caledonia

Philippe Keith, Clara Lord, Laura Taillebois & Pierre Feutry

Muséum national d'Histoire naturelle, UMR BOREA 7208 MNHN-CNRS-UPMC-IRD, DMPA, CP026, 43 rue Cuvier, 75231 Paris Cedex 05, France
keith@mnhn.fr

ABSTRACT

Since 1861, freshwater fishes have been studied at different periods in New Caledonia. The first list was published in 1915, but the major inventories were done between 1998 and 2003. These inventories allowed the discovery of many new species and the publication, in 2003, of the *Atlas of Freshwater fish and crustaceans of New Caledonia*, which listed 64 freshwater fish species. Between 2004 and 2010, additional specific surveys were conducted by the MNHN and 9 species were added. Among them, 3 were new for science. Gobiidae family represents 30% of the freshwater fishes of New Caledonia. This high percentage is explained by their particular life cycle adapted to insular systems.

RÉSUMÉ

Nouvelles données sur les poissons d'eau douce de Nouvelle-Calédonie.

La faune ichtyologique des eaux douces a été étudiée à diverses reprises et à divers degrés en Nouvelle-Calédonie depuis 1861. La première liste des espèces a été établie en 1915, mais c'est entre 1998 et 2003 qu'ont été entrepris les plus gros efforts d'inventaires. Ceux-ci ont donné naissance à la description de plusieurs espèces nouvelles ainsi qu'à la publication, en 2003, de « *l'Atlas des poissons et crustacés d'eau douce de Nouvelle-Calédonie* », qui comprenait 64 espèces de poissons. De nouveaux inventaires menés entre 2004 et 2010 par le MNHN ont porté le nombre d'espèces à 73. Parmi les 9 espèces signalées en plus par rapport à 2003, 3 sont nouvelles pour la science. Les Gobiidae présentent 30% des espèces de poissons connus dans les eaux douces de Nouvelle-Calédonie. Ce fort pourcentage est expliqué notamment par les traits de vie particuliers de ces espèces et leur adaptation aux systèmes insulaires.

INTRODUCTION

Fishes have been studied at different periods in New Caledonia. Jouan (1861, 1863, 1877), Castelnau (1873) and Ogilby (1897) were the first to work on them. Jouan cited only marine and brackish fishes. Castelnau (1873) listed 14 species, a few being freshwater species, collected by Mr Adet from Noumea, but there was no location information. Ogilby (1897) gave a list of 6 freshwater species, but it was not until 1915, with the publication of Weber and de Beaufort's paper, that the first list of freshwater fishes of New Caledonia appeared. This list, containing nearly 30 species, was produced with the samples collected on 26 rivers by Sarasin and Roux between 1911 and 1912. Later, Starmühlner (1968) prospected 42 rivers, but only for molluscs and some crustaceans. In 1991, the PEDCAL expedition organised by the Muséum national d'Histoire naturelle (MNHN), prospected 31 rivers (Séret 1997) and increased significantly the number of collected species.

Finally, between 1998 and 2003, the MNHN conducted, with the provincial and territorial authorities, an exhaustive inventory of freshwater fish (CHLOE expeditions). Inventories were undertaken on the major hydrosystems of Grande-Terre and Loyalties Islands and allowed the discovery of many new species (Keith *et al.* 2000; 2002; Watson *et al.* 2001, 2002, 2005; Marquet *et al.* 2003). At the end of these expeditions, a reference book was published: *the Atlas of Freshwater fish and crustaceans of New Caledonia* (Marquet *et al.* 2003). These inventories were completed between 2004 and 2010 during additional specific studies conducted by the MNHN with the Provinces, particularly in Panié Mountain (2004, 2006, 2010) Poindimié area (2006, 2010) and Bélep Islands (2007) (North Province) (Keith *et al.* 2009a), and Yaté area (2007) and Côte oubliée (2009) (South Province). They led to the discovery of new species (Keith *et al.* 2009b; Keith *et al.* 2010) and of species never caught in New Caledonia.

The purpose of this paper is to update the list of the freshwater fish species of New Caledonia, with a particular insight on amphidromous gobies.

MATERIALS AND METHODS

During 2004-2010, nearly 60 rivers, representing 250 stations, were prospected in both North and South Provinces of New Caledonia.

Investigations were undertaken by Punctual Abundance Sampling (PAS); sampling was done using electrical fishing methods at a large number of randomised points in the streams. The position of the points must respect the proportion of the diversity of run-off habitats. The surface prospected at each point corresponds to the anode's electrical field.

For electrical fishing methods, a current generator was used: a portable machine using a battery with an output power of 180 W. It gives rectangular impulses at a fixed frequency of 100 Hz or 400 Hz. The duty cycle is controllable and is of 5 to 25%. It has three voltage outputs: 150, 200 and 300 V.

Electrical fishing is performed wading upstream, that way the water stays clear in front of the fisherman. The method consists in placing a fishing electrode near shelters in which the animals are found; the electrode creates an electrical field, which has an attraction effect within a radius of a one-metre zone under average conditions. When a fish comes within this field, it is stunned; it can then be caught easily with a hand net.

Each species caught was identified and, when preserved, the material was deposited in the collection of the National Museum of Natural History in Paris.

RESULTS

The 2004-2010 expeditions brought new material and nine new recorded species were caught, compared to the Atlas published in 2003 (Marquet *et al.* 2003). Among them, six widespread species are now known to occur also in New Caledonia and three were recently described as new species. Among the nine new records for New Caledonia, five concern the Gobiidae Sicydiinae subfamily (Teleostei) with two new species.

The new occurrences are: among the Gobiidae, *Stiphodon semoni* Weber 1895, found in North Province (Pouebo), with very few specimens; *Smilosicyopus fehlmanni* (Parenti & Maciolek, 1993) caught in North Province in many rivers,

Redigobius balteatus (Herre, 1935) (Dumbéa river); and among the Syngnathidae, *Microphis argulus* (Peters, 1855). Two new introduced species were also caught locally in some swamps and rivers: *Trichopodus trichopterus* (Pallas, 1770) and *Xiphophorus maculatus* (Günther, 1866). The new species described since 2003 are *Smilosicyopus pentecost* (Keith, Lord & Taillebois, 2010) from Bélep and North Province in New Caledonia and Vanuatu, *Stiphodon mele* Keith, Lord & Pouilly, 2009 from New Caledonia and Vanuatu; both are Gobiidae Sicydiinae, and *Bleheratherina pierucciae* Aarn & Ivantsoff, 2009 (Atherinidae), a freshwater species from South Province rivers.

The updated list of freshwater fishes of New Caledonia is given in Table 1.

TABLE 1

List of Freshwater fish species of New Caledonia. * introduced ; Bold new record.

FAMILIES	SPECIES NAMES
Anguillidae	<i>Anguilla australis</i> Richardson, 1841 <i>Anguilla marmorata</i> Quoy & Gaimard, 1824 <i>Anguilla megastoma</i> Kaup, 1856 <i>Anguilla obscura</i> Günther, 1872 <i>Anguilla reinhardtii</i> Günther, 1872
Moringuidae	<i>Moringua microchir</i> Bleeker, 1853
Ophichthyidae	<i>Lamnostoma kampeni</i> (Weber & de Beaufort, 1916) <i>Lamnostoma orientalis</i> (McClelland, 1844)
Muraenidae	<i>Gymnothorax polyuranodon</i> (Bleeker, 1854)
Galaxiidae	<i>Galaxias neocaledonicus</i> Weber & de Beaufort, 1913
Cyprinidae	<i>Carassius auratus</i> (Linnaeus, 1758) * <i>Cyprinus carpio</i> Linnaeus, 1758 *
Poeciliidae	<i>Poecilia reticulata</i> Peters, 1859 * <i>Xiphophorus hellerii</i> Heckel, 1848 * <i>Xiphophorus maculatus</i> (Günther, 1866) *
Syngnathidae	<i>Microphis brachyurus</i> (Bleeker, 1854) <i>Microphis argulus</i> (Peters, 1855) <i>Microphis cruentus</i> Dawson & Fourmanoir, 1981 <i>Microphis leiaspis</i> (Bleeker, 1853) <i>Microphis retzii</i> (Bleeker, 1856)
Atherinidae	<i>Bleheratherina pierucciae</i> Aarn & Ivantsoff, 2009
Mugilidae	<i>Cestraeus oxyrhynchus</i> Valenciennes, 1836 <i>Cestraeus plicatilis</i> Valenciennes, 1836 <i>Crenimugil crenilabis</i> (Forsskal, 1775) <i>Crenimugil heterocheilos</i> (Bleeker, 1855) <i>Liza melinoptera</i> (Valenciennes, 1836) <i>Chelon planiceps</i> (Valenciennes, 1836) <i>Mugil cephalus</i> Linnaeus, 1758
Ambassidae	<i>Ambassis miops</i> Günther, 1872 <i>Ambassis interrupta</i> Bleeker, 1853
Kuhliidae	<i>Kuhlia marginata</i> (Cuvier, 1829) <i>Kuhlia munda</i> (De Vis, 1884) <i>Kuhlia rupestris</i> (Lacepède, 1802)
Scatophagidae	<i>Scatophagus argus</i> (Linnaeus, 1766)
Centrarchidae	<i>Micropterus salmoides</i> (Lacepède, 1802) *
Cichlidae	<i>Oreochromis mossambicus</i> (Peters, 1852) * <i>Sarotherodon occidentalis</i> (Daget, 1962) *

Belontiidae	<i>Trichogaster pectoralis</i> (Regan, 1910) * <i>Trichopodus trichopterus</i> (Pallas, 1770) *
Microdesmidae	<i>Parioglossus neocaledonicus</i> Dingerkus & Séret, 1992
Eleotridae	<i>Butis amboinensis</i> (Bleeker, 1853) <i>Eleotris acanthopoma</i> Bleeker, 1853 <i>Eleotris fusca</i> (Forster, 1801) <i>Eleotris melanosoma</i> Bleeker, 1852 <i>Hypseleotris cyprinoides</i> (Valenciennes, 1837) <i>Bunaka gyrinoides</i> (Bleeker, 1853) <i>Giuris margaritacea</i> (Valenciennes, 1837) <i>Ophieleotris</i> sp. <i>Ophiocara porocephala</i> (Valenciennes, 1837)
Gobiidae	<i>Awaous guamensis</i> (Valenciennes, 1837) <i>Awaous ocellaris</i> (Broussonet, 1782) <i>Psammogobius biocellatus</i> (Valenciennes, 1837) <i>Glossogobius illimis</i> Hoese & Allen, 2012 <i>Lentipes kaaea</i> Watson, Keith & Marquet, 200 <i>Mugilogobius notospilus</i> (Günther, 1877) <i>Mugilogobius mertonii</i> (Weber, 1911) <i>Redigobius balteatus</i> (Herre, 1935) <i>Redigobius bikolanus</i> (Herre, 1927) <i>Schismatogobius fuligimentus</i> Chen, Séret, Pöllabauer & Shao, 2001 <i>Sicyopterus lagocephalus</i> (Pallas, 1770) <i>Sicyopterus sarasini</i> Weber & de Beaufort, 1915 <i>Smilosicyopus chloe</i> (Watson, Keith & Marquet, 2001) <i>Smilosicyopus fehlmanni</i> (Parenti & Maciolek, 1993) <i>Smilosicyopus pentecost</i> (Keith, Lord & Taillebois, 2010) <i>Sicyopus zosterophorum</i> (Bleeker, 1856) <i>Stenogobius yateiensis</i> Keith, Watson & Marquet, 2002 <i>Stiphodon atratus</i> Watson, 1996 <i>Stiphodon mele</i> Keith, Marquet & Pouilly, 2009 <i>Stiphodon sapphirinus</i> Watson, Keith & Marquet, 2005 <i>Stiphodon semoni</i> Weber, 1895 <i>Stiphodon rutilaureus</i> Watson, 1996
Rhyacichthyidae	<i>Rhyacichthys guilberti</i> Dingerkus & Séret, 1992 <i>Protogobius attiti</i> Watson & Pöllabauer, 1998

BIODIVERSITY OF FRESHWATER FISH IN NEW CALEDONIA

The updated list of freshwater fishes indexes now 73 species versus 64 in the Atlas published in 2003. Among them, 22 species of freshwater gobies are listed (30%), and among the Gobiidae, the Sicydiinae subfamily was the most diverse with 12 species (16.4%) and included: *Sicyopterus sarasini* Weber and de Beaufort, 1915, an endemic; *Sicyopterus lagocephalus* (Pallas, 1774) widely distributed and known from the Comoros and Mascarene Islands in the western Indian Ocean to the Society Islands in French Polynesia and from the Ryukyu Islands of Japan to the Cape York Peninsula of Queensland, Australia (Keith *et al.* 2005; Lord *et al.* 2010); *Sicyopus zosterophorum* (Bleeker, 1857) known from eastern Indian Ocean drainages of Indonesia to Japan and New Caledonia; *Smilosicyopus chloe* (Watson, Keith & Marquet, 2001) from New Caledonia and Vanuatu (Watson *et al.* 2001); *Smilosicyopus fehlmanni* (Parenti & Maciolek, 1993) from Palau to New Caledonia; *Smilosicyopus pentecost* (Keith, Lord & Taillebois, 2010) from New Caledonia and from Vanuatu; *Stiphodon atratus* Watson, 1996 and *Stiphodon rutilaureus* Watson, 1996 known from eastern Indonesia, Vanuatu to New Caledonia (Watson 1996); *Lentipes kaaea* Watson, Keith & Marquet, 2002 known from New Caledonia, Futuna, Fiji and Vanuatu; *Stiphodon sapphirinus* Watson, Keith & Marquet, 2005 known from New Caledonia and Vanuatu; *Stiphodon mele* Keith, Lord & Pouilly, 2009 known from New Caledonia and Vanuatu; and the widespread *Stiphodon semoni* Weber, 1895.

Like most Pacific islands, New Caledonia is characterised by the absence of indigenous primary and secondary fishes that are intolerant to saltwater *sensu* Myers (1949) and Banarescu (1990). As a consequence of the absence of primary and

secondary native fishes, the rivers are then mainly colonised by diadromous fish (migrant amphihaline species performing a part of their biological cycle in freshwaters). These are represented by two categories: catadromous (Anguillidae (eels)) and amphidromous fish (Gobiidae, Eleotridae and Rhyacichthyidae).

Amphidromous gobiids have a life cycle adapted to the conditions of insular rivers subject to extreme climatic and hydrological seasonal variation. These species spawn in freshwaters, the free embryos drift downstream to the sea where they undergo a planktonic phase (dispersal phase), before returning to the rivers to grow and reproduce (McDowall 1997; Keith 2003; Keith *et al.* 2006). These gobies contribute most to the diversity of fish communities in the Indo-Pacific insular systems, and have the highest levels of endemism (Lord & Keith 2006, 2008; Keith & Lord 2011a; 2011b; Keith *et al.* 2011). Therefore, it is not surprising that Gobiidae represent 55.5% of the new records.

ACKNOWLEDGMENTS

We would like to thank all the partners that have financially supported this work, that is, the New Caledonian Government and the National Museum of Natural History of Paris (PPF “Ecologie fonctionnelle et développement durable des écosystèmes naturels et anthropisés” and Leg Prevost) for the PhD fellowship; BIONEOCAL ANR (P. Grandcolas); the Fondation de France. We also thank the New Caledonian North and South Provinces (J.-J. Cassan, J. Manauté and C. Méresse) for allowing sampling (permit No 1224-08/PS). This study was made possible through assistance in sampling expeditions or with the help of colleagues in all the areas studied: G. Marquet, C. Flouhr, P. Gaucher, G. Ségura, P. Lim, and F. Busson.

REFERENCES

- BANARESCU P. 1990 — Zoogeography of freshwater. General distribution and dispersal of freshwater animals. Aula Verlag ed., Wiesbaden, vol. 1, 511 p.
- CASTELNAU F. DE 1873 — Contribution to the ichthyology of Australia, VII. Fishes of New Caledonia, *Proceeding of Zoological Acclimatation Society of Victoria* 2: 110.
- JOUAN H. 1861 — Note sur quelques espèces de poissons de la Nouvelle-Calédonie. *Mémoires de la Société des sciences naturelles de Cherbourg* 8.
- JOUAN H. 1863 — Supplément à la description des poissons de la Nouvelle-Calédonie. *Mémoires de la Société des sciences naturelles de Cherbourg* 9.
- JOUAN H. 1877 — Quelques mots sur la faune ichthyologique de la côte N.-Est d'Australie et du détroit de Torrès, comparée à celle de la Nouvelle-Calédonie. *Mémoires de la Société des sciences naturelles de Cherbourg* 21.
- KEITH P. 2003 — Biology and ecology of amphidromous Gobiidae in the Indo-Pacific and the Caribbean regions. *Journal of Fish Biology* 63(4): 831-847.
- KEITH P. & LORD C. 2011a — Tropical freshwater gobies: Amphidromy as a life cycle, in Patzner R.A., Van Tassell J.L., Kovacic M. & Kapoor B.G. (eds.), *The Biology of Gobies*, Science Publishers Inc, 685 pp.
- KEITH P. & LORD C. 2011b — Systematics of Sicydiinae in *The Biology of Gobies* (R.A. Patzner, J.L. Van Tassell, M. Kovacic & B.G. Kapoor ed.), Science Publishers Inc, 685 pp.
- KEITH P., WATSON R. & MARQUET G. 2000 — Découverte d'*Awaous ocellaris* (Broussonet, 1782) (perciformes, gobiidae) en Nouvelle-Calédonie et au Vanuatu. *Cybium* 24(4): 345-400.
- KEITH P., WATSON R.E. & MARQUET G. 2002 — *Stenogobius* (insularigobius) *yateiensis*, a new species of freshwater goby from New Caledonia (Teleostei: Gobioidae). *Bulletin Français de Pêche et Pisciculture* 364: 187-196.
- KEITH P., GALEWSKI T., CATTANEO-BERREBI G., HOAREAU T. & BERREBI P. 2005 — Ubiquity of *Sicyopterus lagocephalus* (Teleostei: Gobioidae) and phylogeography of the genus *Sicyopterus* in the Indo-Pacific area inferred from mitochondrial cytochrome b gene. *Molecular Phylogenetics and Evolution* 37(2005): 721-732.
- KEITH P., LORD C. & E. VIGNEUX, 2006 — In vivo observations on postlarval development of freshwater gobies and eleotrids from French Polynesia and New Caledonia. *Ichthyological Exploration of Freshwater* 17: 187-191.
- KEITH P., MARQUET G. & POUILLY M. 2009a — *Stiphodon mele*, a new species of freshwater goby from Vanuatu and New Caledonia (Teleostei: Gobiidae: Sicydiinae), and comments about amphidromy and regional dispersion. *Zoosystema* 31(3): 471-483.
- KEITH P., LORD C., MARQUET G. & KALFATAK D. 2009b — Biodiversity and biogeography of amphidromous fishes from New Caledonia, a comparison to Vanuatu in GRANDCOLAS P. (ed.), *Zoologica Neocaledonica* 7. Biodiversity studies in New Caledonia, *Mémoires du Muséum national d'Histoire naturelle* 198: 175-183.
- KEITH P., LORD C. & TAILLEBOIS L., 2010 — *Sicyopus* (*Smilosicyopus*) *pentecost*, a new species of freshwater goby from Vanuatu and New Caledonia (Teleostei: Gobioidae: Sicydiinae). *Cybium* 34(3): 303-310.
- KEITH P., LORD C., LORION J., WATANABE S., TSUKAMOTO K., CRUAUD C., COULOUX A. & DETTAI A. 2011 — Phylogeny and biogeography of Sicydiinae (Teleostei: Gobioidae) inferred from mitochondrial and nuclear genes. *Marine biology* 158(2): 311-326.
- LORD C. & KEITH P. 2006 — Threatened fishes of the world: *Protogobius attiti* (Watson and Pöllabauer, 1998) (Galaxiidae). *Environmental Biology of Fishes* 77: 101-102.

- LORD C. & P. KEITH 2008 — Threatened fishes of the world: *Sicyopterus sarazini* Weber & De Beaufort (Gobiidae). *Environmental Biology of Fishes* 83: 169-170.
- LORD C., BRUN C., HAUTECOEUR M. & KEITH P. 2010 — Comparison of the duration of the marine larval phase estimated by otolith microstructural analysis of three amphidromous *Sicyopterus* species (Gobiidae: Sicydiinae) from Vanuatu and New Caledonia: insights on endemism. *Ecology of Freshwater fish* 19: 26-38.
- MARQUET G., KEITH P. & VIGNEUX E. 2003 — Atlas des poissons et crustacés d'eau douce de la Nouvelle-Calédonie. *Collection Patrimoines naturels*, MNHN, Vol. 58, Paris, 282 p.
- Mc DOWALL R.M 1997 — Is there such a thing as amphidromy? *Micronesica* 30(1): 3-14.
- MYERS G.S. 1949 — Salt tolerance of freshwater fish groups in relation to zoogeographical problems. *Bijdr. Dierkunde* (Leiden) 28: 315-322.
- OGILBY J.D. 1897 — A contribution to the zoology of New Caledonia. *Proceedings of the Linnean Society of N.S. Wales* 22(4): 762-770.
- SÉRET B. 1997 — Les poissons d'eau douce de Nouvelle-Calédonie: implications biogéographiques des récentes découvertes. *Zoologica neocaledonica, Mémoires du Muséum national d'Histoire naturelle* 171(4): 371-378.
- STARMÜLHNER F. 1968 — Études hydrobiologiques en Nouvelle-Calédonie (mission 1965 du Premier Institut de Zoologie de l'Université de Vienne). I. Généralités et descriptions des stations. *Cahiers ORSTOM, série Hydrobiologique* 2(1): 3-27.
- VERON J.E.N. 1995 — Corals in space and time. The biogeography and evolution of the Scleractinia. University of New South Wales Press, Sydney.
- WATSON R. E. 1996 — A review of *Stiphodon* from New Guinea and adjacent regions, with descriptions of five new species (Teleostei: Gobiidae: Sicydiinae). *Revue Française d'Aquariologie* 23: 113-132.
- WATSON R.E., KEITH P. & MARQUET G. 2001 — *Sicyopus* (*Smilosicyopus*) *chloe*, a new species of freshwater goby from New Caledonia (Teleostei: Gobioidae: Sicydiinae). *Cybium* 25(1): 41-52.
- WATSON R.E., KEITH P. & MARQUET G. 2002 — *Lentipes kaaea*, a new species of freshwater goby from New Caledonia (Teleostei: Gobioidae: Sicydiinae). *Bulletin Français de Pêche et Pisciculture* 364: 173-185.
- WATSON R.E., KEITH P. & MARQUET G. 2005 — *Stiphodon sapphirinus*, a new species of freshwater goby of New Caledonia (Teleostei: Gobioidae: Sicydiinae). *Cybium* 29(4): 339-345.
- WEBER M. & DE BEAUFORT L. F. 1915 — Les poissons d'eau douce de la Nouvelle-Calédonie, in SARASIN F. & ROUX J. (eds), Nova Caledonia. Recherches scientifiques en Nouvelle-Calédonie et aux Iles Loyalty. *Zoology* 2(1): 17-41..

The New Caledonian and Fijian species of Aterpini and Gonipterini (Coleoptera: Curculionidae)

Guillermo Kuschel

7 Tropicana Drive - Mt Roskill - Auckland 1041 - New Zealand
g.kuschel@xtra.co.nz

ABSTRACT

The species of Aterpini and Gonipterini from New Caledonia and Fiji are revised, the Aterpini represented by seven species of *Acanthoapterus* from New Caledonia, the Gonipterini by ten species of *Pterogonius* from New Caledonia and two from Fiji. *Acanthoapterus* is transferred from Eugnomini to Aterpini, and *Pterogonius* n. gen. (type species *P. millei* n. sp.) is proposed for the species of Gonipterini. Aterpini is a Gondwanic element occurring in Australia, New Zealand, New Guinea and New Caledonia as well as in southern Chile and Argentina. Gonipterini is an Australasian element extending its distribution to Fiji. Hosts of most species of either group remain to be determined except for *Dracophyllum* (Ericaceae) as host of *Acanthoapterus inermis* and *Syzygium cumini* (Myrtaceae) as host of *Pterogonius kanalensis*. *Amphionotus undulatus* n. sp., belonging to the already revised New Caledonian Entiminae, is described and added as an appendix.

RÉSUMÉ

Les espèces d'Aterpini et Gonipterini (Coleoptères ; Curculionidae) de Nouvelle-Calédonie et des Fidji.

Les espèces d'Aterpini et de Gonipterini de Nouvelle-Calédonie et les îles Fidji sont révisées. Les Aterpini sont représentés par sept espèces d'*Acanthoapterus* en Nouvelle-Calédonie, les Gonipterini par dix espèces de *Pterogonius* en Nouvelle-Calédonie et deux à Fidji. *Acanthoapterus* est transféré des Eugnomini aux Aterpini et *Pterogonius* n. gen. (espèce type *P. millei* n. sp.) est proposé pour les espèces de Gonipterini. Aterpini est un groupe gondwanien se trouvant en Australie, Nouvelle-Zélande, Nouvelle-Guinée et Nouvelle-Calédonie, ainsi que dans le sud du Chili et de l'Argentine. Les Gonipterini sont un groupe australasien étendant sa distribution aux îles Fidji. Les hôtes de la plupart des espèces de chaque groupe restent à déterminer, sauf pour *Dracophyllum* (Ericaceae) en tant qu'hôte d'*Acanthoapterus inermis* et *Syzygium cumini* (Myrtaceae) en tant qu'hôte de *Pterogonius kanalensis*. *Amphionotus undulatus* n. sp., appartenant aux Entiminae néocalédoniens déjà révisés, est décrite et ajoutée en annexe.

INTRODUCTION

The species of Aterpini and Gonipterini of Curculionidae of New Caledonia and Fiji are the subject of this paper. Although the two tribes are adequately defined, their position in a particular subfamily remains uncertain. A discussion about placement of these groups is left out here as of no greater relevance to the main object of this study.

The procedures and the acronyms are the same as explained in Kuschel (2008). Several more species of Entiminae have been received since, amongst them one which is described as an appendix to this paper.

SYSTEMATIC PART

Family CURCULIONIDAE Latreille, 1802

Tribe ATERPINI Lacordaire, 1863

This tribe is represented in New Caledonia by seven species of the genus *Acanthopterus* Faust, two of them described by Montrouzier in the Palearctic genus *Trachodes* Germar. These two species were transferred in the catalogue of Gemminger and Harold (1871) to the genus *Scolopterus* White of the tribe Eugnomini. When Faust (1889) proposed *Acanthopterus* for them he left the genus in the same tribe Eugnomini where it stayed till now. The relationship of *Acanthopterus* is with the *Pelororhinus*-group of Aterpini from Australia.

Genus **ACANTHOPTERUS** Faust, 1889

Acanthopterus Faust, 1889: 67. This study: n. transf. (from Curculioninae: Eugnomini).

Type species. *Trachodes penicillatus* Montrouzier, 1861, by original designation.

DESCRIPTION — Eyes transversely ovate, surrounded above, behind and below by a groove, in dorsal view maintaining curvature of contour of head capsule; forehead usually a little narrower than rostrum, with shallow transverse impression and a central fovea; rostrum about as long as prothorax, with a laterodorsal furrow on either side joining frontal furrow; epistome neither raised nor depressed; mandibles decussate, dentate, with 1 or 2 punctules but no obvious hairs or setae; scrobes deep, directed obliquely downwards, amply visible in dorsal view, with pterygia somewhat protruding over the sides; antennae mostly median, scape not reaching eyes, funicle 7-segmented, segment 2 distinctly longer than 1, segments 3-7 longer than wide, not increasing in width towards club; club elongate-ovate, apparently 4-segmented. Prothorax about as long as wide, bisinuous at base, gently rounded, weakly constricted at apex, longitudinally convex, with large, postocular lobes, covering part of eyes when rostrum bent down. Elytra variable in shape, sculpture and vestiture, with or without tubercles. Prosternum flat, or with shallow rostral canal; mesosternal process not wider than antennal club; metasternum between middle and hind legs longer than diameter of a mid-coxa; ventrite 2 from behind coxal cavity longer than 1. Fore coxae spherical, contiguous, distinctly postmedian; femora rather weakly incrassate, unarmed; all tibiae on lower edge with a fringe of dense short hairs directed apicad, with transverse but no dorsal comb, with small mucro more or less obscured by hairs; tarsi wide, first three segments densely padded with adhesive pile, segment 3 wider than 2, deeply bilobed; onychium passing segment 3 by a length of lobes, with divaricate claws. Tergites well pigmented, reddish-brown or piceous, medially undivided, 5-7 with pruinose patches; spiracles on membrane lightly darkened with microtrichia.

Male. Tergite 7 with straight, slightly converging sides on basal two thirds, truncate or subemarginate, basal angles enclosing the spiracles auriculate, basal half smooth, apical half finely to gradually more coarsely punctate towards apex, with short, semierect pilosity; tergite 7 only slightly exposed beyond 7. Sternite 8 well pigmented, narrowly divided into

two slightly transverse, truncate plates, apex fringed with rather long hairs; sternite 9 robust, with well developed or with rudimentary arms, without lobes. Tegmen with well pigmented ring and apodeme, with no or only short parameral lobes. Aedeagus about as long as abdomen on midline (incl. process); pedon distinctly shorter than apodemes, rounded or emarginate at apex, with pale window on sides; tectal area clear; internal sac long, reaching to or extending beyond apex of apodemes or, variously sclerotised at base, sometimes with ventral diverticulum, inner walls with finer and coarser vestiture from near base of pedon to a short distance before basal sclerite, cephalad from base sometimes with a tapering long membranous extension; ejaculatory duct inserting dorsally at a median lobe of a basal sclerite.

Female. Tergite 7 auriculate at basal angles, tapering in straight line to apical quarter, broadly truncate at apex, heavily pigmented on sides and apical half, on basal half much more lightly pigmented on median area and even lighter on pruinose patches, coarsely and densely punctate and pilose, hairs becoming gradually longer; tergite 8 concealed under 7, tapering with gentle curve, truncate, reddish-brown on sides and apical quarter, finely punctate, sparsely pilose. Hemisternites 0.5x as long as sternite 8, proximal ones reduced to struts, distal ones pale but distinctly pigmented, tapering to a blunt point, with 3-4 moderately long setae; stylus apical, rather robust, 1.5x as long as wide, slightly widening apicad, with a longish seta on either side. Vagina very long; bursa short, narrow, not constricted at base; spermatheca slender, slightly wider at base of stem, with long apical hook; gland long, about 5x longer than spermatheca; duct relatively short, about 3x as long as spermatheca, inserting ventrally at base of bursa against oviduct.

DISTRIBUTION — New Caledonia.

HOSTPLANT — All the species of *Acanthopterus* are likely to be associated with particular species or genera, but hardly any hosts were specified by collectors. The only safe association is *Dracophyllum verticillatum* (Ericaceae) for *A. inermis*, and possible associations are *Melaleuca* (Myrtaceae) for *A. tristis* and *Hibbertia* (Dilleniaceae) for *A. velatus*.

ETYMOLOGY — The generic name *Acanthopterus* is derived from the Greek ákantha meaning spine or thorn, and pterón meaning wing or elytron.

REMARKS — Faust (1889) designated *Trachodes penicillatus* Montrouzier as type species of *Acanthopterus*. The original description of the species was unequivocally based on two specimens of two different species, one with a brush on the elytra (*A. penicillatus*), the other with a tooth (*A. bidens*). The Collection J. Faust is housed in the Staatmuseum für Tierkunde, Dresden, which has no specimens of *A. penicillatus*, but has one of *A. bidens* whose identity was kindly confirmed by Dr Olaf Jaeger (pers. com. 22 March 2010). In accordance with Article 70.3 of the Code of Nomenclature, *A. penicillatus* (Montrouzier) is here confirmed as type species of *Acanthopterus* Faust.

KEY TO SPECIES OF ACANTHOPTERUS

1. Prothorax without a prosternal canal. Elytra in lateral view level with pronotum. 2
 – Prothorax with a prosternal canal flanked by low carinae. Elytra in lateral view rising at basal area to a flat top 6
2. Elytra with tubercles 3
 – Elytra without tubercles. 5.8-9.8 mm. New Caledonia *A. inermis*
3. Elytra with a tubercle on interstria 3 4
 – Elytra with a tubercle on interstria 5. 6.2-8.0 mm. New Caledonia *A. bidens*
4. Tubercles of elytra without a brush of long hairs on top 5
 – Tubercles of elytra with a brush of long hairs on top. 61-8.2 mm. New Caledonia *A. penicillatus*

5. Interstriae lacking granules. Tubercles on elytra bulbous, shiny, glabrous. Rostrum on underside in male with a pair of teeth behind mouthparts. 6.5-9.3 mm. New Caledonia *A. lugubris*
 – Interstriae with granules. Tubercles on elytra compressed, dull, with recumbent short hairs. Rostrum on underside in male without a pair of teeth behind mouthparts. 7.4-8.5 mm. New Caledonia *A. granulosus*
6. Antennal insertions median, approximately on middle of rostrum. Elytra sparsely squamose, leaving most of integument uncovered. 7.1-9.8 mm. New Caledonia *A. tristis*
 – Antennal insertions distinctly postmedian, on basal third of rostrum. Elytra densely squamose, scales covering integument completely. 10.5-12.0 mm. New Caledonia *A. velatus*

Acanthopterus bidens n. sp.

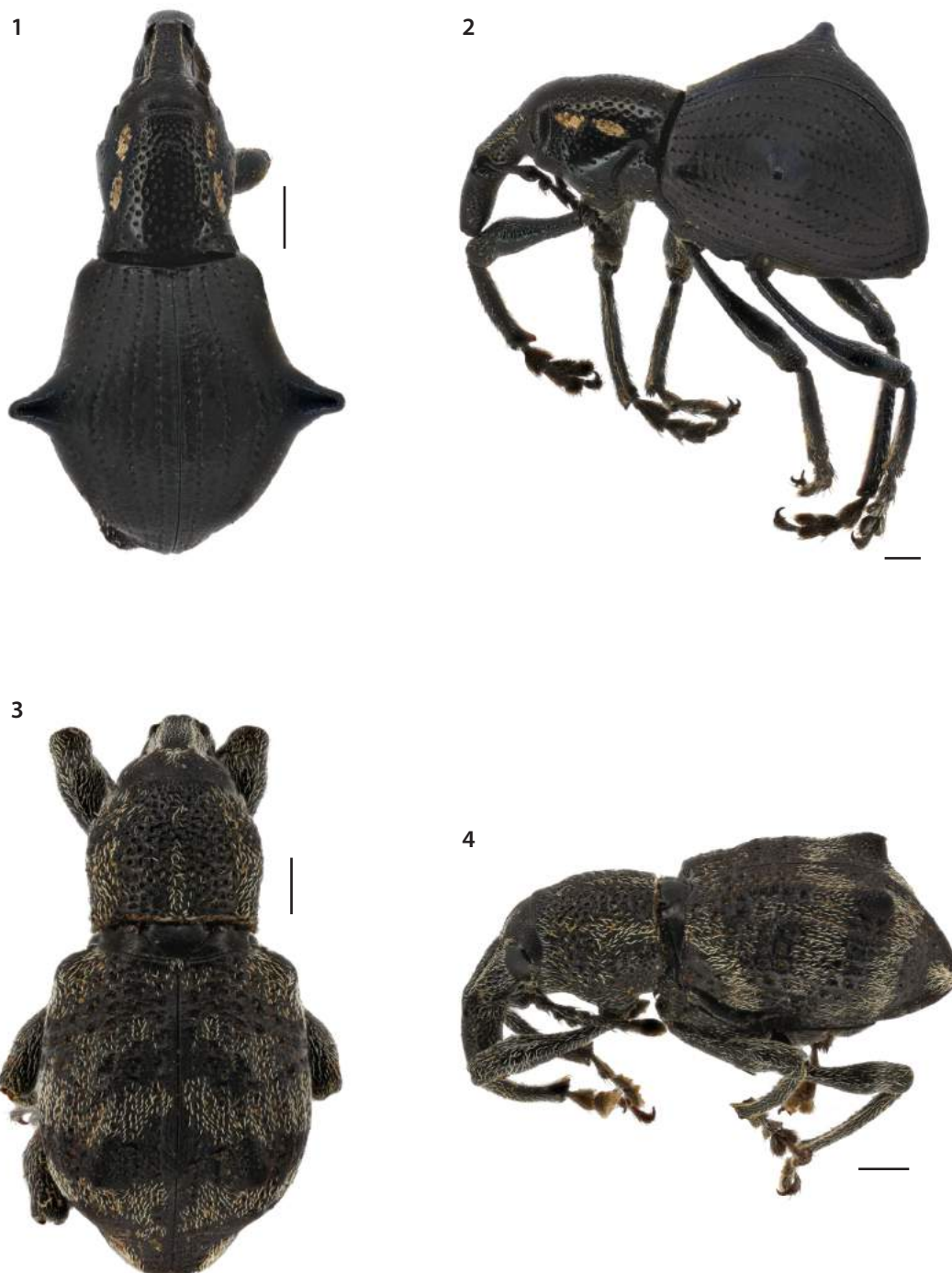
Figures 1, 2

TYPE MATERIAL — Holotype male: New Caledonia, 7.5x 5.2 (across elytral teeth), Col de la Pirogue, 330 m, 14 Feb 1963, G Kuschel & CM Yoshimoto, in NZAC, Auckland. Paratypes, 24 specimens in BPBM, MNHN, MNHW, NZAC, QMBA, SMTD, SRFP: New Caledonia. Balade, 1 male, Montrouzier [as *A. penicillatus* in error], coll. Fauvel; Mt Mandjélia, 20°40'S 164°52'E, 550-600 m, 1 male, 19 Nov 2008, M Wanat; Tes Dawenia, 1 female, 12 Nov 2010; La Guen, 2 females, 20 Nov 2010, C. Mille; La Guen, 1 female, 24 Nov. 2010, J. Brinon; Aoupinié, sawmill, 21°11'S 165°16', 950-1000 m, 2 males, 1 female, 8 Feb 2004, M Wanat; Aoupinié, 21°09'S 165°19'E, 500 m, 1 female, 2 Jan 2005, G Monteith; Aoupinié (Goipin rd junction), 21°10'S 165°18'E, 730 m, 1 female, 17 Jan 2007, M Wanat & R Dobosz; Aoupinié, 21°11'S 165°17'E, 650-700 m, 1 male, 19 Jan 2007, M Wanat; E. Col d'Amieu, Sarraméa, 1 female, 21 Nov 2005, Cazeres & Nugues; Sarraméa, Col d'Amieu, 1 male, 2-28 Dec 2005, Cazères, Mille & Kataoui; Col d'Amieu, 21°58'S 1165°77'E 450 m, 1 male, 14 Nov 2008, M Wanat; Mt Humboldt, 1350 m, 1 male, 10-11 Feb 2005, S Cazères & C Mille; Mt Koghi, 1 male, Feb 1962, NLH Krauss; Forêt de Thi, 1 male, 2 Feb 1967; Col de la Pirogue, 330 m, 2 males, 14 Feb 1963, G Kuschel & CM Yoshimoto; Haute Rivière Bleue, 22°04'S 166°37'E, 330-560 m, 1 female, 21 Dec 2006, M Wanat; 'New Caledonia', 1 female, [as *Acanthopterus penicillatus*], Faust Coll., (pers. com. O. Jaeger, Dresden, March 2010).

HOSTPLANT — Unknown.

ETYMOLOGY — The species name *bidens* is a Latin noun for double tooth.

DESCRIPTION — Integument blue or black, shiny, elytra dull with alutaceous minisculpture, dorsally almost entirely glabrous. Vestiture consisting of a broken stripe of broad pale scales on either side of pronotum imbedded in depressions, a pale line from inner margin of eyes to top of scrobes, broad scales on fore and middle coxae, on prosternum above and in front of coxae, and behind lower part of postocular lobes; legs, especially tibiae with pale and black hairs; male with erect hair on middle of meso and metasternum, and ventrites 1 and 5. Head and forehead with moderately fine punctation, forehead not depressed across, with or without frontal fovea. Rostrum 1.13-1.14x longer than prothorax, 3.10-3.18x longer than wide at apex; postrostrum straight up to pterygia, cylindrical, straight, a little more coarsely punctate than vertex; prorostrum slightly widening apicad, gradually less coarsely punctate than postrostrum, underside in both sexes lacking tubercle. Antennae with hairs and setae black, club brown; first segment of funicle asymmetrical, strongly knobby. Prothorax in male slightly (1.05x) longer than wide, in female as wide as long, distinctly indented closely to basal angles at a deep and broad downwards going groove, widest at apical one/quarter, usually with weak constriction for collar, strongly convex across, a little less convex lengthwise, with moderately coarse puncta, these on basal half spaced mostly by more than their diameter, on apical half becoming gradually denser and coarser towards apex, on flanks in front of deep large groove nearly smooth, with only widely spaced puncta, denser on collar. Scutellum variable from elongate to oval or transverse, smooth, devoid of vestiture. Elytra at shoulders 1.23x wider than prothorax, 1.9x longer



FIGURES 1-4

1-2, *Acanthoapterus bidens*, holotype male, 7.7 mm, Col de la Pirogue; 3-4, *A. granulosus*, holotype female, 8.5 mm, Baie du Sud. Scale bars = 1 mm.

than combined width, across spines approximately as wide as long, widening considerably to middle, gently convex across, in lateral view considerably deeper at middle, straight between base and middle, gently convex on apical declivity. Striae relatively narrow, first two or three partly sulcate, 4 and 5 interrupted in the middle by tooth; interstriae several times wider than striae, flat, stria 5 with prominent, outwards directed tooth projecting well over elytral sides. Metasternum between middle and hind coxae weakly convex. Ventriles finely, sparsely punctate. Hind legs in male passing tip of elytra, in female not quite extending to tip. All tibiae slightly curved in both sexes.

Length 6.2-8.0 mm.

REMARKS — *A. bidens* is unique by having a tubercle on interstria 5 instead of 3, a deep, broad groove on the flanks of the prothorax from the top in front of the basal angles halfway down to the fore coxae, and in the male for the presence of long erect hairs on the underside. As Montrouzier specifically stated that one of at least two specimens possessed outwards directed spines in one of the sexes, he consequently had a specimen of *A. bidens* as well, which has not been located.

Acanthopterus granulosus n. sp.

Figures 3, 4

TYPE MATERIAL — Holotype female: New Caledonia, 8.5x3.9 mm, Baie du Sud, Coll. Fauvel, as *Acanthopterus tristis* Montr. (in Fauvel's writing), in IRSN, Brussels. Paratypes, 8 specimens in BPBM, IRSN, MNHW, NZAC: New Caledonia. Balade, 1 male, Montrouzier, Coll. Fauvel; La Guen, 1 male, 20 Nov 2010, C. Mille; Pic d'Amoa, 20°56'S 165°s7'E, 100-220 m, 1 female, 14 Jan 2007, M Wanat; Aoupinié, 780-1000 m, 1 pair, 8 Feb 2004, M Wanat; Aoupinié, 21°17'S 165°31'E, 700 m, 1 female on juvenile *Araucaria columnaris*, 27 Nov 2008, M Wanat; Col des Pirogues, 330 m, 2 males, 21 Feb 1963, G Kuschel & CM Yoshimoto.

HOSTPLANT — Unknown.

ETYMOLOGY — The epithet *granulosus* is Latin for studded with small granules.

DESCRIPTION — Integument black, sometimes with bluish tint, tarsi piceous, prothorax and elytra dull, rostrum shiny. Vestiture consisting of sparse recumbent white hair and lineal or lanceolate scales, forming on prothorax a vague lateral stripe and on elytra usually vague bands before and after tubercle, a band running down from base of interstriae 5 and 6 behind callus towards hind coxae and a spot on either side low down on declivity. Head with dense, moderately fine punctation. Forehead with slightly coarser punctation, a fovea, and in lateral view a shallow sinus. Rostrum as long as prothorax and 2.8-2.9x as long as wide at apex and 1.1-1.2x wider than forehead, curved; postrostrum cylindrical, straight, coarsely punctate, with a shallow dorso-lateral furrow; prorostrum curved, coarsely punctate at first, gradually less so towards apex; underside behind mouthparts without tubercles. First segment of funicle very short, strongly asymmetrical, widening considerably on one side, all segments with white hair and black setae; club brown. Prothorax 1.06x wider than long, gently rounded, with distinct constriction at apex, longitudinally convex, densely, coarsely punctate, without deep groove on basal third of flanks. Scutellum with minute puncta and hair. Elytra at shoulders 1.3x as wide as prothorax and 1.6-1.8x longer than wide, at widest point 1.4-1.5x longer than wide, widening in straight line to middle, then rounded to apex, not humped, rather flat, shoulders with enhanced callus. Striae about as wide as interstriae, punctation at basal third usually as large as on prothorax but deeper; interstriae roughened with minute piliferous granules, interstria 3 beyond middle at top of declivity with a slightly elongate and finely granulose tubercle topped with short black hair. Prosternum without traces of a rostral canal. Metasternum

between middle and hind coxae nearly flat. Entire underside with distinct, sparse punctation. Femora moderately incrassate, in male passing, in female not reaching tip of elytra.

Length 7.4-8.5 mm.

REMARKS — The specimen from Balade is one of two marked as type of *A. tristis* Montrouzier apparently in Fauvel's writing. The true *A. tristis* has a deep dorsolateral furrow on the postrostrum, a rather symmetrical first segment of the funicle, a low, elongate, not bulbiform tubercle on interstria 3, a distinct though rather shallow rostral canal in front of forecoxae, and scales instead of hairs.

Acanthopterus inermis Heller, 1916

Figures 5, 6

Acanthopterus inermis Heller, 1916: 314

TYPE MATERIAL — Holotype female: New Caledonia: nr summit of Mt Humboldt, 1600 m, 18 Sep 1911, F Sarasin & J Roux in SMTD, Dresden (not seen).

MATERIAL EXAMINED — New Caledonia (Mt Humboldt, Mt Mou, Haute Rivière Bleue). 11 specimens. other specimens in BPBM, MNHN, MNHW, NZAC.

HOSTPLANT — *Dracophyllum verticillatum* (Ericaceae, formerly Epacridaceae), a montane species occurring above 700 m of altitude.

ETYMOLOGY — The epithet *inermis* is Latin for unarmed named so for lack of tubercles on elytra.

DESCRIPTION — Integument blue, or black with bluish tint, shiny except for alutaceous minisculpture on elytra. Vestiture of white lines of lineal or oblong white scales, one line from inner margin of eyes to top of scrobes in a shallow furrow, one on either side of pronotum and one above fore coxae; short black hair in striae and on interstriae; white hair and black setae on antennae and legs. Head and forehead finely punctate, forehead with fovea. Rostrum as long as wide or up to 1.14x longer, 3.04 to 3.44x longer than wide at apex, cylindrical, straight, coarsely punctate on basal half, rather abruptly curving down from top of scrobes at apical half and gradually more finely punctate towards apex on apical half; underside in both sexes without tubercle in both sexes. Antennae inserting on middle or a little before middle; segment 1 of funicle hardly any wider than 2, this 2.3x longer than 1, segment 7 slightly longer than wide. Prothorax 0.90 to 1.05x as long as wide, gently rounded on sides, weakly constricted at apex, in male longitudinally weakly, in female strongly convex, on midline smooth in part, rather coarsely punctate, puncta separated by shiny interspaces. Scutellum smooth, glabrous. Elytra at shoulders approximately 1.4x wider than prothorax, 1.3 to 1.4x as long as wide at middle, strongly inflated, in lateral view considerably more convex and higher than prothorax, dull with alutaceous minisculpture; striae considerably narrower than interstriae, puncta much smaller than on pronotum. Underside nearly smooth, minutely punctate; prosternum flat; hind legs in male passing elytra, in female not reaching tip of elytra; some or all tibiae curved.

Length 5.8-9.8 mm.

REMARKS — *A. inermis* is characterised by inflated, considerably heightened elytra and lack of tubercles and scales on elytra. Five specimens collected by me in 1963 from the host alongside two Molytini species of *Dracophyllus* Kuschel at about 1000 m altitude.



FIGURES 5-8

5-6, *A. inermis*, female, 8.8 mm, Mt Mou; **7-8**, *A. lugubris*, holotype male, 7.8 mm, Mt Koghi. Scale bars = 1 mm.

***Acanthopterus lugubris* n. sp.**

Figures 7, 8

TYPE MATERIAL — Holotype male: New Caledonia, 7.8x3.9 mm, Mt Koghi, 500-700 m, 1 male, 29 Jan 1963, G Kuschel, in NZAC. Paratypes: 26 specimens in ANIC, BPBM, IRSN, MNHN, MNHW, NZAC, SMTD, SRFP: New Caledonia. Mandjélia, summit, 20°24'S 164°32'E, 780 m, 2 males, 13 Dec 2004, G Monteith; Mandjélia (Ouégoa), 20°39'S 164°53'E, 787 m, 1 female, 8 Feb 2005, on Araliaceae, S Cazères & C Mille; Mandjélia, summit, 750-780 m, 1 female, 10 Jan 2007, M Wanat & R Dobosz; Mt Panié, 800 m, 1 female, 27-29 Jul 1971, on *Freycinetia*, JL Gressitt; Mt Panié, 950-1600 m, 1 pair, 14-16 May 1984, G Monteith & D Cook; Mt Panié, 20°33'S 164°46'E, 1300 m, 1 male, 2 Feb 2004, M Wanat; Pic d'Amoa, 20°58'S 165°17'E, 480 m, 1 pair, 3 Jan 2005, GB Monteith; Aoupinié, 21°11'S 165°16'E, 950-1000 m, 1 female, 8 Feb 2004, Aoupinié, 21°11' 165°18'E, 750 m, 1 male, 2 May 2005, G Monteith, Aoupinié, 700-900 m, 1 male, 18 Jan 2007, M Wanat & R Dobosz; Aoupinié 21°11'S 165°18'E, 650-800 m, 1 pair, 19 Jan 2007, M Wanat; Aoupinié (gate), 900-950 m, 1 male, 21 Nov 2007, M Wanat; Aoupinié (refuge), 21°15'S 165°32'E, 400 m, 1 female, 29 Nov 2008, M Wanat; Aoupinié (Goipin road junction), 21°18'S 165°30'E, 700-750 m, 1 male, 29 Nov 2008, M Wanat; Dzumac Mts, (Mt Ouin road junction) 22°02'S 165°28'E, 900 m, 1 male, 28 Dec 2006, M Wanat & R Dobosz; Kanala, 1 male, coll. Fauvel; Sarramea, Col d'Amieu, 21°35'S 165°48'E, 1 male, 18 Oct 2006, S Cazères; same locality, 1 male, 18 Nov 2005, Cazères & Mille; Mt Humboldt, 950 m, 1 male, 16 Feb 2005, S Cazères & C Mille; Haute Rivière Bleue, 22°05'S 166°38'E, 280-330 m, 2 pairs, 24-28 Jan 2004, M Wanat.

HOSTPLANT — Unknown. One specimen beaten from Araliaceae, another from *Freycinetia* (Pandanaceae), thus an association with these two plant families is not yet established and best ignored.

ETYMOLOGY — The species name *lugubris* is a Latin adjective meaning sombre.

DESCRIPTION — Integument dull or shiny, black or piceous, occasionally with bluish tint, antennae, tarsi and underside reddish brown. Vestiture variable, consisting of sparse recumbent white or yellowish-brown hair or piliform, lineal and elliptic scales, vestiture usually a little denser laterally on prothorax and across elytra at base and at front and back of tubercles. Head and forehead finely punctate and pubescent, forehead 1.27-1.33x narrower than rostrum at apex, transversely impressed, with central fovea. Rostrum 0.91-1.05x as long as prothorax (lower range for male) and 2.69-2.89x longer than wide at apex; postrostrum cylindrical, straight, moderately coarsely punctate, with shallow latero-dorsal furrow; prorostrum curved, with gradually finer punctation; underside in male with a prominent tooth on either side behind maxillae. Segment 1 of funicle moderately clavate, 2nd segment 1.5-1.6x longer than 1, remainder of segments slightly longer than wide. Elytra at shoulders 1.20-1.27x wider than prothorax and 1.78-2.03x longer than own width, 1.39-1.62x longer than at widest point, widening in almost straight line to middle, flat across first three interstriae, longitudinally flat from base to middle or beyond, not humped, with gentle declivity. Striae wide, uneven, about as wide as interstriae at base, with puncta of variable size, usually coarser and deeper than on pronotum; interstriae a little uneven, partly transversely rugose, with a bulky, bulbiform tubercle on interstria 3 with its base impinging on interstriae 2 and 4, the tubercle occasionally reddened and with fine punctation and inconspicuous hair on top. Prosternum flat, without a rostral canal. Metasternum rounded off in front of hind coxae. Underside very finely and sparsely punctate along median areas, punctation a little coarser at sides. Femora weakly incrassate, hind ones in male passing in female not reaching tip of elytra; all tibiae in male curved, hind ones in female usually straight.

Length 6.5-9.3 mm.

REMARKS — *A. lugubris* is defined by the following combination of characters: absence of a prosternal canal, presence of low, not humped or inflated elytra, a bulbiform tubercle on interstria 3, and in male a prominent small tubercle on either side behind mouthparts on the underside.

Acanthopterus penicillatus (Montrouzier, 1861)

Figures 9, 10

Trachodes? penicillatus Montrouzier, 1861: 888*Scolopterus penicillatus* - Gemminger & Harold 1871: 2490*Acanthopterus penicillatus* - Faust 1889: 67

TYPE MATERIAL — Described from two specimens, only one located fitting description as well as name. Lectotype male: New Caledonia, 6.1 x 2.9 mm, *Trachodes penicillatus* (mihi), Balade, type, Montrouzier det. 1860, Coll. Fauvel, in IRSN.

MATERIAL EXAMINED — Other specimens in ANIC, BPBM, IRSN, MNHW, NZAC, SMTD, SRFP. **New Caledonia** (Balade, Mt Mandjélia, La Guen, Aoupinié, Col des Roussettes, Col de la Pirogue, Mt Koghi, Forêt de Thy, Rivière Bleue Park, Pic du Grand Kaori, Forêt Nord), 24 specimens.

HOSTPLANT — Unknown.

ETYMOLOGY — The specific epithet *penicillatus* is Latin for brushed.

DESCRIPTION — Integument blue of variable intensity, largely shiny, elytra dull. Head with a double row of piliform scales from inner edge of eyes to middle of rostrum on top of scrobes; prothorax with four stripes of white scales, one on either side of disc, other on flank above fore coxae; similar scales at end of interstria 10, anteriorly on sides of metasternum and in front of hind coxae. Head finely, densely punctate, with black inconspicuous pubescence. Forehead slightly depressed transversely, more coarsely punctate than on vertex and with similar pubescence. Rostrum 1.05-1.08x longer than prothorax, 3.2-3.6x longer than wide at apex; postrostrum cylindrical, straight in lateral view, considerably more coarsely punctate than forehead and vertex except under scaly lines; prorostrum slightly widening apicad, distinctly less coarsely punctate, underside in male with tubercle on either side behind maxillae. Antennae with white or black hairs

**FIGURES 9-10**

A. penicillatus, female, 7.2 mm, Col des Roussettes. Scale bars = 1 mm.

and black setae, club velvety brown; first segment of funicle strongly asymmetrical by considerably widening at apical two-thirds to one side. Prothorax slightly (appr. 1.05x) longer than wide, slightly widening in straight line to middle, then gently rounded towards a weak collar, strongly convex across, less convex lengthwise, shiny, coarsely punctate, with short black pubescence; basal one-third of flanks lacking deep groove. Scutellum finely punctate, with short hairs or small scales. Elytra at shoulders 1.3-1.5x wider than prothorax, 1.7-1.8x longer than own combined width, widening conspicuously in straight or slightly convex line to middle, rather flat dorsally on first three interstriae, in lateral view considerably deeper (higher) on middle and straight between base and middle, apical declivity weakly convex. Striae with deep piliferous puncta, these puncta separated by flat or rugose intervals at same level with interstriae but depressed when first two or three striae sulcate; interstriae flat except for 10th subcostate at posterior end; 1-3 widening appreciatively towards middle, third one with an elongate tubercle on middle topped with a tuft or brush of erect hairs, dorsal interstriae with very fine and sparse low piliferous granules. Ventrites finely, sparsely punctate, 5 more densely and coarsely so, not impressed in either sex. Hind legs in male extending beyond body. All tibiae slightly curved in either sex.

Genitalia. See generic description above.

Length 6.1-8.2 mm.

REMARKS — *A. penicillatus* is defined by having a brush of long hairs on top of a tubercle on interstria 3. Montrouzier evidently had at least two specimens, one with a brush, the other with an outwards directed spine, differences he took to be sexual.

***Acanthopterus tristis* (Montrouzier, 1861) n. comb.**

Figures 11-14

Trachodes tristis Montrouzier, 1861: 889.

Scolopterus tristis - Gemminger & Harold 1871: 2491.

TYPE MATERIAL — Two syntypes located representing two distinct species (see *A. granulosus* above), the larger one here designated as the type for better conforming with the size of 10mm given in the original description. Lectotype female: New Caledonia, 9.5x4.7 mm, Balade, *Acanthopterus tristis* [apparently in Fauvel's writing], type, Coll. Fauvel, in IRSN, Brussels.

MATERIAL EXAMINED — Non-type specimens in BPBM, MNHN, MNHW, NZAC, QMBA, SFRP. **New Caledonia** (Balade, Mandjélie/Ouégoa, La Guen, Pic d'Amoa, Col des Roussettes, Col d'Amieu, Aoupinié, Mt Humboldt, Plateau de Dogny, Haute Rivière Bleue). 34 specimens.

HOSTPLANT — Unknown; one specimen beaten off flowering *Melaleuca* (Myrtaceae) by me is a possible host.

ETYMOLOGY — The specific epithet *tristis* is Latin standing for sad.

DESCRIPTION — Integument piceous, shiny. Vesture of yellow scales surrounding eyes above, behind and below; white pubescence in laterodorsal furrows of rostrum and legs, some white or pink scales on femora. Head with dense, rather coarse punctation, with scales surrounding eyes above, behind and below but not in front; pubescence inconspicuous, black or grey, short but long enough to go over intervals to adjacent puncta. Forehead transversely sulcate, with central fovea, as coarsely punctate as vertex. Rostrum as long as prothorax, 3.5x or more longer than wide at apex; postrostrum cylindrical, straight, with rather deep laterodorsal furrows merging with frontal sulcus; prorostrum curved, gradually more finely punctate towards apex, without a pair of tubercles behind mouthparts on underside. Prothorax in female as long as prothorax, in male slightly (1.03x) longer, rounded on sides, with weak constriction at collar, longitudinally rather



FIGURES 11-14

11-12, *A. tristis*, male, 7.4 mm, Mandjélia (type variant, with more prominent elytral tubercle); 13-14, *A. tristis*, male, 9.3 mm, Plateau de Dogny. Scale bars = 1 mm.

strongly convex, flanks without deep groove near base. Scutellum finely punctate, usually with scales. Elytra at shoulders 1.43-1.52x wider than prothorax and 1.6-1.7x longer than own width, at widest point 1.55-1.59x longer, parallel-sided or slightly widening to middle, longitudinally flat, not heightened to middle. Striae a little narrower than interstriae, mostly with shallow puncta; interstriae slightly convex, usually only slightly raised at end of dorsum, occasionally raised to a low tubercle, with abundant flat granules. Prosternum with lower edge of postocular lobes extended over collar towards coxae forming a shallow rostral canal. Metasternum ending abruptly in front of hind coxae. Femora moderately incrassate, hind ones in male usually passing, in female not reaching tip of elytra; all tibiae curved in male, hind ones straight in female.

Length 7.1-9.8 mm.

REMARKS — The lectotype is in relatively good condition; it was initially pinned and then mounted on its side on a card. *A. tristis* shares with *A. velatus* a shallow prosternal canal and differs in size, position of antennal insertions and vestiture.

***Acanthopterus velatus* n. sp.**

Figures 15, 16

TYPE MATERIAL — Holotype female: New Caledonia, 12.0x5.25 mm, Mt Dzumak Road (7th km), 22°05'S 166°27'E, 700 m, 1 female, 9 Feb 2004, on *Hibbertia lucens* in maquis, M Wanat, in MNHN, Paris. Paratype: Col de Yaté, 22°17'S 166°09'E, 380 m, 1 female, 2 Dec 2008, M Wanat, in MNHW.

HOSTPLANT — *Hibbertia lucens* (Dilleniaceae), a likely host.

ETYMOLOGY — The specific epithet *velatus* is Latin for covered or dressed, named so because of the rather dense squamose covering on the body.

DESCRIPTION — Integument piceous, head, rostrum and prothorax black, shiny. Vestiture squamose, elytra mostly with dense grey and brown round scales, with oblique bands of white scales, one a little behind humeral callus from interstria 7 to sutural stria at the end of dorsum, other alongside posterior end of metepisternum from interstria 10 to sutural stria at apical third, white scales also at the apex of elytra, on the sides and midline of pronotum. Head and forehead densely squamose; forehead 1.4x wider than rostrum at apex, weakly depressed across against base of rostrum, with large fovea



FIGURES 15-16

A. velatus, holotype female, 12.0 mm, Mt Dzumac. Scale bars = 5 mm.

filled with scales at bottom. Rostrum 1.18x longer than prothorax and 5.33x longer than its width at apex; postrostrum cylindrical, straight dorsally, curving slightly ventrally, with shallow, densely squamose dorso-lateral furrow, dorsal surface densely punctate, scales on dorsal surface distinctly smaller than on pronotum; prorostrum as long as postrostrum between antennal insertions and front margin of eyes, gently widening from middle to apex and to antennal insertion area, punctation gradually decreasing in size towards apex. Scrobes directed towards lower quarter of eyes. Prothorax as long as wide, rounded on sides, weakly constricted at apex, strongly convex; scales on midline and sides large, ovate, those in dark stripes and a dark spot on middle of sides smaller, leaving large part of integument visible. Scutellum completely covered with broad, imbricate scales. Elytra at shoulders 1.53x wider than prothorax and 1.75x longer than own width, parallel-sided, with rounded off rectangular shoulders, raised at base to a flat dorsum; striae fine, considerably narrower than interstriae, most puncta concealed by scales; interstriae 3 and 5 distinctly more convex, rather subcostate, lacking tubercles. Underside and legs, including first three segments, densely squamose. Prosternum with a shallow rostral canal flanked by low carinae. Femora moderately incrassate; tibiae curved; segment 1 of tarsi distinctly larger than 2. Length 10.5-12.0 mm.

REMARKS — *A. velatus* is the largest species of the genus and is easily distinguished by dense vestiture covering the entire body, by its distinctly postmedian insertion points of the antennae, a long prorostrum and a funicle nearly three times longer than the scape.

Tribe GONIPTERINI Montrouzier, 1861

The New Caledonian and Fijian species agree with typical Australian forms in having a distinct posthumeral swelling or knob on interstria 10, an unusually short proventriculus with externally weak, hardly noticeable apodemal ridges, a distinctive type of sternite 8 in females, but differ in having divaricate claws, coarsely faceted eyes, membranous tergites 1 to 6, and lack parameral lobes or wax exudates. A host association with Myrtaceae seems to be a further point of agreement with the Australian Gonipterini. According to the list of Jaffré *et al.* (2001), the family Myrtaceae is richly represented in New Caledonia with more than 20 genera and well over 200 species. A recent transfer of Gonipterini from Cyclominae to Curculioninae by R. Oberprieler (2010) is probably premature as Cyclominae cannot be defined neither against Entiminae or against Curculioninae. Oberprieler suggested to have the ambit of the taxon restricted to those with an ovipositor suited to laying eggs in soil and crevices, a character of doubtful phylogenetic significance as it only reflects adaptation to a particular environment and applies only to one sex.

***PTEROGONIUS* n. gen.**

Type species. *Prypnus artensis* (Montrouzier, 1861)

DISTRIBUTION — New Caledonia, Fiji.

HOSTPLANT — Those with known association are on Myrtaceae; larvae not known, not seen on leaves, thus presumed to be endophytic somewhere on the host.

ETYMOLOGY — *Pterogonius* is a Greek compound from pterón for wing, and gonía for angle, in fact just a simple inversion of the components of the generic name *Gonipterus*; gender masculine.

DESCRIPTION — Head round, not constricted. Eyes convex, coarsely faceted. Rostrum moderately long, transversely convex dorsally; prorostrum (area between antennal insertions and apex) with a major seta on either side of epistome and a similar seta on genae behind mandibular sockets, without any vestiture on dorsal surface. Antennae, when folded back, directed to lower half of eyes; scapes slender, clavate at apical third, passing front margin of eyes, occasionally extending to middle of eyes; first two segments of funicle of similar length; club slender, long, usually 3 to 4x as long as wide, loosely articulated. Prothorax parallel-sided at basal two-thirds, dorsally even or with shallow depressions, bisinuous at base, weakly constricted at apex, without distinct ocular lobes and cilia. Scutellum elongate, level with surrounding elytral surface, leaning against prothorax; in brachypterous species distinctly smaller and rounded. Elytra parallel-sided or tapering, much wider than prothorax, sinuous and proclinate at base, on either side between scutellum and shoulders curving forward against prothorax. Interstriae 1, 3, 5 flat or with low tubercles, 10 with posthumeral knob. Fore coxae slightly antemedian, contiguous or disjunct; mesosternal process sloping caudad, not knobby; metasternum longitudinally convex, in lateral view rounded off in front of hind coxae, not dentiform. Femora pedunculate, clavate. Tibiae on lower edge with variously sized denticles, usually with mucro and premucro. Claws divaricate, strongly recurved, in view from behind looking much like open pincers with incurving prongs. Hind wings (in fully winged species) with long *M*, without veins between *Cu* and *A4*, lacking also vein *A5* and anal cell. Tergites 1-6 clear, unpigmented, though very lightly so at times on 5 and 6 on pruinose patches; tergite 7 pigmented, finely ciliate at apex, densely pubescent. Proventriculus very short; blades only with fine armature, lacking large, heavily chitinised teeth; externally with very weak apodemal ridges.

Male. Tergite 8 partly exposed beyond 7; sternite 8 divided into two contiguous plates. Tegmen with complete ring, long apodeme, and no parameral lobes. Aedeagus as long as or slightly longer than venter; pedon reddish brown, somewhat translucent, with rolled up sides to dorsal level or slightly over on dorsal surface; tectum unpigmented except for ostial valves; internal sac well exposed between apodemes, with large, solid basal sclerite, an open, inverted U-shaped sclerite near ostium, plus extensive, very fine wall vestiture; ejaculatory duct inserting dorsally and caudad from base of internal sac onto basal sclerite.

Female. Ventrite 5 simple, without a blunt, submarginal edge below the proper, denticulate margin of other gonipterines. Hemisternites relatively narrow, conical, with very sparse short hairs; stylus apical, tapering, curving slightly outwards; bursa not obvious beyond oviduct; spermathecal duct inserting on base of oviduct.

REMARKS — The main differences with *Gonipterus* are: head without a postocular constriction, coarsely faceted eyes, divaricate claws, presence of only one anal vein, lack of anal cell, lack of teeth on proventricular blades, and lack of parameral lobes. Twelve species are present, ten from New Caledonia, two from Fiji.

KEY TO SPECIES OF *PTEROGONIUS*

1. Elytra on dorsum lacking tubercles and tufts of hairs 2
— Elytra on dorsum with tubercles or tufts of hairs 6
2. Without a preapical callus at end of interstria 5 3
— With a preapical callus at end of interstria 5 5
3. Fore coxae contiguous 4
— Fore coxae disjunct. 6.5-6.8 mm. New Caledonia *P. alticola*
4. Integument black; most of dorsal surface concealed under ochrous and white scales; striae very shiny, with large and small puncta. 5.7-7.0 mm. New Caledonia *P. sylviae*
— Integument reddish brown, most of dorsal surface free of scales except for some white ones on sides of pronotum and on two thirds of basal area of elytra between interstriae 4 and 10 of dense, largely imbricating white scales. 4.7 mm. Fiji *P. albomaculatus*

5. Elytra with a white transverse macula on either side of middle. Rostrum flat at apex. Striae about as wide as interstriae. 4.5-5.8 mm. New Caledonia *P. artensis*
 — Elytra lacking a white macula on middle but with a white spot on base of interstria 5 and 6 against humeral callus. Rostrum transversely convex at apex. Striae much narrower than interstriae. 5.0-5.1 mm. New Caledonia *P. tabularis*
6. Fore coxae contiguous. Elytra widest across posthumeral knob 7
 — Fore coxae disjunct. Elytra widest across laterally projecting shoulders. Length 6.5-8.7 mm. New Caledonia *P. kanalensis*
7. Eyes separated by distinctly more than half a rostrum width 8
 — Eyes separated by distinctly less than half a rostrum width. 5.0-5.4 mm. Fiji *P. vitiensis*
8. Interstria 9 squamose throughout 9
 — Interstria 9 on middle section behind pothumeral knob glabrous, smooth and shiny 10
9. Interstria 3 with three low tubercles, 3.9-4.8 mm. New Caledonia *P. wanati*
 — Interstria 3 with two tubercles. 4.5-5.2 mm. New Caledonia *P. fauveli*
10. Metasternum between middle and hind coxae distinctly shorter than a mid-coxal; diameter. 6.5-7.1 mm. New Caledonia *P. tardus*
 — Metasternum between middle and hind coxae distinctly longer than a mid-coxal diameter 11
11. Eyes symmetrical, weakly produced, evenly convex. 5.4-7.1 mm. New Caledonia *P. millei*
 — Eyes asymmetrical, strongly produced, unevenly convex. 4.9 mm. New Caledonia *P. bryophilus*

***Pterogonius albomaculatus* n. sp.**

Figure 17

TYPE MATERIAL — Holotype male: Fiji, 4.7 x 2.1 mm, Viti Levu, Nadarivatu, 762 m, 1 male, 6 Mar 1977, JC Watt and J Kumar, in NZAC.

HOSTPLANT — Unknown; specimen obtained by beating at night.

ETYMOLOGY — The epithet *albomaculatus* is Latin to refer to the large white scaly humeral patch on the elytra.

DESCRIPTION — Integument, including antennae and legs, reddish brown, metepisternum a little darker. Vestiture consisting of extremely fine pubescence on rostrum, most of pronotum and elytra, sparse white scales on midline and sides of pronotum, dense, in part imbricating white scales on basal two-thirds of elytra between striae 3 and 10, and a line beyond junction of interstriae 3 and 5; scales on underside white, lineal on metasternum and venter, broader scales on pro and mesosternum; tibiae on lower edge with long, robust, curved setae. Head coarsely punctate. Eyes moderately convex. Forehead slightly narrower than in other species, 0.65x as wide as rostrum at base, densely, coarsely punctate, without fovea. Rostrum 1.10x as long as prothorax, 2.4x as long as wide at apex, punctation on postrostrum less coarse than on head; prorostrum with much finer punctation, without hairs or scales apart from a seta. Scape passing front margin of eyes without reaching middle; club 2.9x longer than wide, terminal segment 0.64x as long as other two segments together. Prothorax 1.18x wider than long, with straight parallel sides, with laterally well marked apical collar; slightly convex lengthwise, coarsely subrugosely punctate. Scutellum covered in dense pili-form white scales. Elytra at shoulders 1.51x wider than prothorax and 1.75x longer than own combined width, across

posthumeral knobs 1.63x longer than wide, slightly converging towards apical third, then attenuated to blunt apex; in lateral view weakly convex and gently declivous; striae much narrower than interstriae, stria 9 wider and deeper, especially alongside venter; interstriae even, flat, without tubercles or preapical callus, 9 and 10 alongside ventrite 5 raised to weak costae. Fore coxae contiguous. Tibiae curved, with equally large mucro and premucro, distinctly denticulate and setose on lower edge. Metasternum in lateral view ending high and slightly overhanging in front of hind coxae.

Length 4.7 mm.

REMARKS — *P. albomaculatus* agrees well with the characters of the genus. It is easily separated from all other species by its fine, inconspicuous pubescence and presence of a large macula of white scales in the humeral area.

***Pterogonius alticola* n. sp.**

Figure 18

TYPE MATERIAL — Holotype female: New Caledonia, 6.5x 3.4 mm, Mt Dzumac (Mt Ouin road junction), 22°03'S 166°47'E, 910 m, 28 Oct 2009, at night, M Wanat, in MNHN. Paratype: Mt Humboldt 1350 m, 1 female, 10/11 Feb 2005, S Cazères and C Mille; in SRFP.

HOSTPLANT — Specimens obtained by beating.

ETYMOLOGY — The specific name *alticola* is a noun in apposition to mean a dweller of heights.

DESCRIPTION — Integument for most part of a dark or reddish brown, on humeral area and posthumeral knob shiny black. Vestiture squamose, mostly of lineal and piliform scales on head, rostrum, prothorax and legs, of wider and denser scales on elytra where leaving humeral area, posthumeral knob and part of interstriae 8 and 9 bare, on dorsum either uniformly yellowish ochre or with bare patches before and after middle and on sides of preapical callus area. Head shiny, punctulate. Eyes moderately convex. Forehead sparsely punctate, with or without fovea. Rostrum robust, 1.40-1.68x shorter than prothorax, 1.5-1.68x as long as wide at apex, more coarsely and densely punctate than head, prorostrum rather declivous, very finely punctate and shiny, with a few lineal scales and some very short hairs on genae besides a long seta. Scape reaching middle of eyes; club very slender, 4x longer than wide, terminal segment one-third shorter than other two segments together. Prothorax as long as wide or 1.18x wider than long, parallel-sided to before gentle apical collar, coarsely, subrugosely punctate; scales on and near midline shorter, yellowish, directed cephalad. Scutellum greyish, with dense, fine, piliform scales. Elytra across posthumeral knob 1.79-1.84x wider than prothorax and 1.35x as long as wide at shoulders, at first conspicuously widening towards posthumeral knob, then visibly converging apicad; in lateral view rather strongly convex; striae fine, much narrower than interstriae but much coarser on glabrous patches; interstriae even, without tubercles. Fore coxae disjunct, separated by less than width of antennal club, process and sternellum also slightly disjunct. Tibiae strongly curved, with large sharp teeth of about the size of mucro, premucro distinctly larger than mucro and teeth.

Length 6.5-6.8 mm.

REMARKS — *P. alticola* is distinctive on account of its disjunct fore coxae, strongly curved tibiae with heavily armed teeth, wide, triangularly shaped elytra with strongly projecting posthumeral knobs on sides, narrow striae, even interstriae and imbricate scales of a yellowish ochre.

Pterogonius artensis (Montrouzier, 1861) n. comb.

Figure 19

Prypnus? artensis Montrouzier (*Rhinaria?* in footnote), 1861: 887.

TYPE MATERIAL — Holotype female: New Caledonia, 4.8x2.3 mm, *Prypnus artensis* (mihi), Art [in Montrouzier's writing]; in IRSN, Brussels.

MATERIAL EXAMINED — Other specimens in IRSN, MNHN, MNHW, NZAC, QMBA, SRFP. Iles Belep (I. Art, 19°43'S 163°39'E). New Caledonia (Mandjélia, Chagrin, Kaala-Gomen, Thio, Dzumac Mts, Pic du Grand Kaori, Forêt Nord, Col des deux Têtons). 14 specimens.

HOSTPLANT — Unknown.

ETYMOLOGY — The specific epithet *artensis* derived from Art Island, and the suffix *-ensis* commonly used for geographical names.

DESCRIPTION — Dark brown, antennae and legs a shade lighter. Vestiture ochrous except for a white macula on either side of middle of elytra between striae 3 and 6, scales on pronotum sparse, distinctly larger than those on elytra, underside and legs with lineal white scales except for a few ochrous ones on sides of metasternum, pleurites and legs. Head with moderately coarse puncta. Eyes strongly convex. Forehead with scales as elongate and large as on midline of pronotum. Rostrum robust, short, 1.5x shorter than prothorax, 1.6x longer than wide at apex, with punctation similar to that on head and forehead; prorostrum finely punctate, flat and rather declivous in lateral view, sides (genae) with few hairs besides a long seta. Scape reaching middle of eyes; club 3.3x longer than wide, terminal segment 0.44x as long as remainder of club. Prothorax 1.7x wider than long, basal two-thirds parallel, collar constriction weak; dorsally transversely convex, densely, coarsely punctate, most of integument exposed. Scutellum finely pubescent. Elytra 1.55x wider than prothorax, 1.5x longer than their combined width, longitudinally convex; posthumeral knobs slightly showing on sides; striae about as wide as interstriae, puncta deep, these evenly spaced; interstriae even, 5th with low preapical callus, sometimes hardly noticeable (see Figures 17-19, 24).

Length 4.5-5.8 mm.

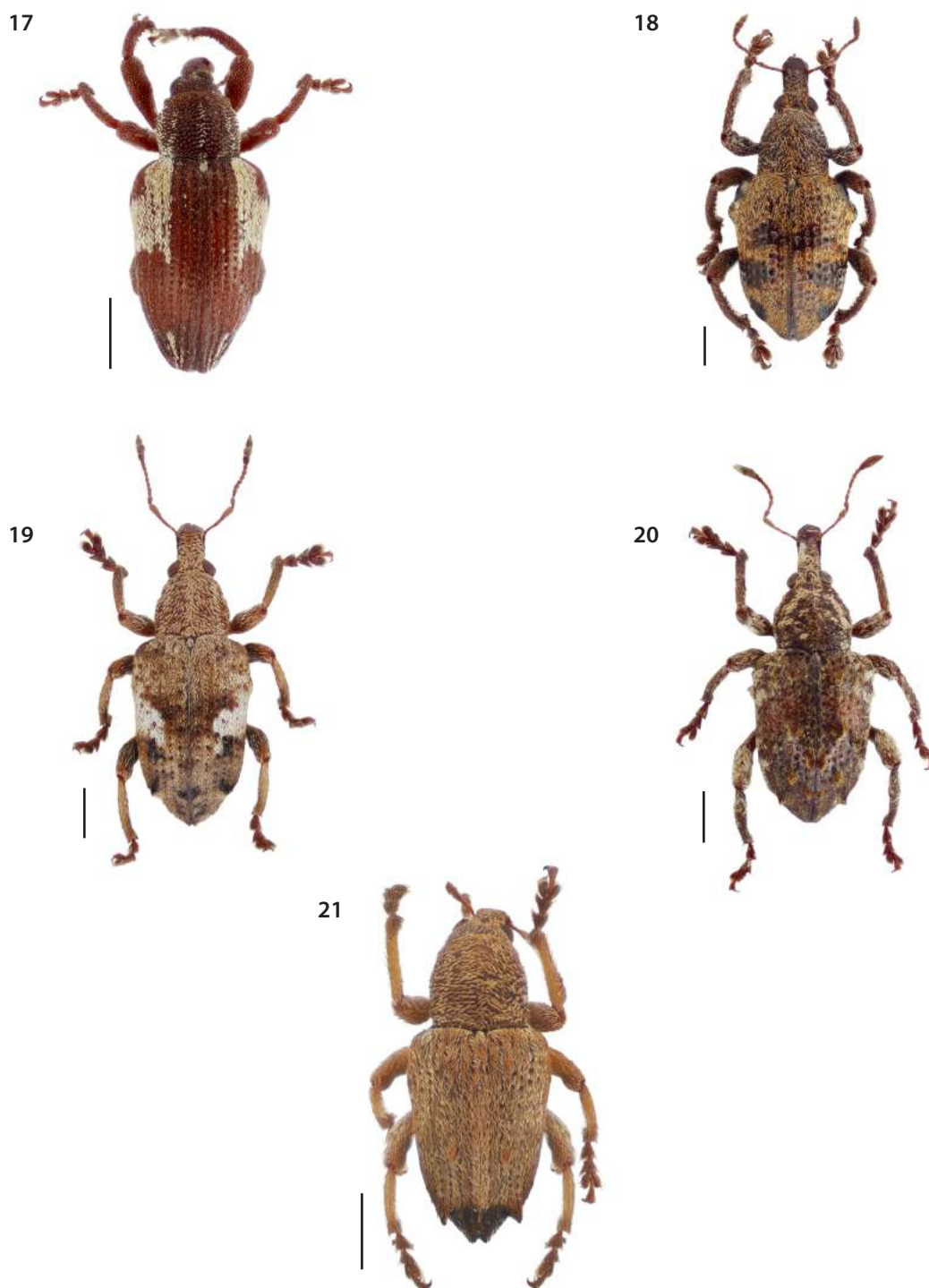
REMARKS — *P. artensis* is defined by the following combination of characters: overall dullness, contiguous forecoxae, even elytra with a white macula on other side of middle and short, apically flat rostrum. The holotype specimen was originally pinned, then mounted on a card, has three-quarters of the right elytron missing but is otherwise in rather good condition. The footnote as *Rhinaria* ?, under the original description, was apparently added by Fauvel.

Pterogonius bryophilus n. sp.

Figure 20

TYPE MATERIAL — Holotype female: New Caledonia, 4.9x2.45 mm, Mandjélia, summit, 20°23'S 164°31'E, 750-780 m, 1 female, 19 Jan 2007, M Wanat & R Dobosz, in MNHN.

DESCRIPTION — Piceous, antennae, tarsi and part of elytra reddish brown. Vestiture squamose, moderately dense, scales variable in shape and size, longer, white scales on head, forehead and rostrum, on two stripes on either side of prothorax, dots on elytral sides and parts of legs; tubercles and preapical callus topped with rusty and deep brown tufts. Head with moderately large punctation, with long, lineal scales. Eyes strongly protruding, asymmetrical, more prominent



FIGURES 17-21

17, *Pterogonius albomaculatus*, holotype male, 4.7 mm, Nadarivatu, Viti Levu; **18**, *P. alticola*, holotype female, 6.5 mm, Mt Dzumac; **19**, *P. artensis*, 5.2 mm, Mt Dzumac; **20**, *P. bryophilus*, holotype, 4.9 mm, Mandjélia; **21**, *P. fauveli*, holotype female, 4.5 mm, Baie de Prony. Scale bars = 1 mm.

posteriorly. Forehead 0.80 of width of rostrum at apex, medially smooth, without fovea, punctate and scaly against eyes. Rostrum 1.3x shorter than prothorax, 2.0x longer than wide at apex, basal half with dense, large, elongate white scales, apical half glabrous, finely punctulate on whole of prorostrum; genae lacking scales. Scape not reaching middle of eyes, slightly curved outwards at apex, segment 1 of funicle a little longer than 2; club 3.4x longer than wide, ratio of segments 7: 9: 13. Prothorax 1.15x wider than long, gently widening in straight line to middle; apical half converging to a rather weakly marked collar; disc longitudinally and transversely slightly convex, with low bosses and depressions, densely, coarsely punctate. Scutellum elongate with fine piliform scales.

Elytra across posthumeral knobs 1.60x wider than prothorax, 1.5x longer than own maximum width, gently tapering on sides and converging to a relatively narrow apex. Striae regular, as wide as interstriae; interstriae 1, 3, 5 with tufted tubercles, two on interstria 1, three on 3, and one on 5 apart from a preapical callus, interstria 9 rather less conspicuously glabrous and shiny. Metasternum distinctly longer than a mid-coxal diameter, flat, low in front of hind coxae. Femora weakly clavate; tibiae incurved at apex, with mucro, with indistinct premucro and nearly smooth lower edge.

Length 4.9 mm.

HOSTPLANT — Unknown. Specimen beaten in montane rainforest.

ETYMOLOGY — The specific name *bryophilus* is a Greek adjective derived from brýon for moss and phílos for liking.

REMARKS — *P. bryophilus* is defined principally by strongly protruding eyes and six tufted tubercles on either elytron.

***Pterogonius fauveli* n. sp.**

Figure 21

TYPE MATERIAL — Holotype female: New Caledonia, 4.5x1.9 mm, Baie de Prony, 22°19'S 165°50'E, Coll. Fauvel, in IRSN, Brussels. Paratypes: Paita-Mou, 300 m, 1 female, 8 Nov 1978, J L Gressitt, in BPBM; Nlle Calédonie, 1 female, in poor condition, Coll. Fauvel., NZAC.

HOSTPLANT — Unknown.

ETYMOLOGY — The species is dedicated to Charles Adolphe Albert Fauvel (1840-1921) who was since his early years fascinated by New Caledonia, with particular interest in the species described by Montrouzier.

DESCRIPTION — Integument dark or pale reddish brown, femora and tibiae usually with light greenish tint. Scales dense, not imbricate, relatively large, elongate and variable in size on elytra yellowish brown. Head densely, coarsely punctate, with long, yellowish brown lineal scales. Eyes rather strongly convex. Forehead 0.90x as wide as rostrum at apex, lacking fovea, its scales larger than on head and rostrum. Rostrum short, 1.12x longer than wide at apex; postrostrum as coarsely punctate as forehead and head, with low median carina and long narrow scales; prorostrum weakly declivous, about as coarsely punctate as ommatidia, with piliform scales on genae. Scape reaching middle of eyes; club 2.6x as long as wide, terminal segment 0.65x as long as other two segments together. Prothorax 1.05x wider than long, subparallel, gently constricted at apex; transversely and longitudinally convex, densely and coarsely punctate, scales distinctly larger than on elytra, all transverse or on midline directed forward. Scutellum densely squamose. Elytra across posthumeral knobs 1.48x wider than prothorax, 1.55x longer than own maximum width, converging in straight line to apical third, then curving in to a slightly bicuspid apex. Striae much narrower than interstriae, stria puncta not quite as coarse as on pronotum, stria 9 not or hardly wider than others; interstria 3 with two tufted tubercles, a low one on basal one/seventh, the other higher on middle, with a yellow or brown tuft, interstria 5 with a prominent, acutely tufted preapical callus.

Forecoxae contiguous. Metasternum between middle and hind coxae distinctly convex or nearly flat. Tibiae slightly in-curved at apex, lower edge denticulate or slightly asperate, all tibiae with mucro and premucro; femora and tibiae without long semierect white setae.

Length 4.5–5.2 mm.

REMARKS — *P. fauveli* is characterised by having only two tubercles on interstria and no tubercles on 5 not counting a preapical callus.

Pterogonius kanalensis (Perroud, 1865) n. comb.

Figure 22

Gonipterus kanalensis Perroud, 1865: 157.

TYPE MATERIAL — Twelve syntypes located. Lectotype male: New Caledonia, 8.0 x 4.9 mm, *Gonipterus kanalensis* Perroud, Kanala, Coll. B Perroud, in MNHN; paralectotypes in IRSN, MNHN, NHML.

MATERIAL EXAMINED — Canala, Aoupinié, Dzumac, Forêt Nord, La Foa, Yahoué. 37 specimens, in ANIC, BPBM, MNHW NZAC, QMBA, SRFP.

HOSTPLANT — *Syzygium cumini* (Myrtaceae); larvae not yet seen.

ETYMOLOGY — The species name refers to the type locality Canala in its earlier spelling with an initial K.

DESCRIPTION — Integument reddish brown, head, rostrum and legs darker. Vestiture squamose, greyish brown, rather dense; elytral tubercles usually topped with variously coloured scaly tufts; interstriae 10 and 11 alongside venter, femora, tibiae and sides of metasternum and ventrites with long, semierect white setae; underside to a good extent with long, appressed, lineal white scales. Head with moderately large squamiform puncta. Eyes moderately convex. Forehead 0.70 as wide as rostrum at apex, transversely convex, without distinct fovea. Rostrum robust, 1.52x shorter than prothorax, 1.8x as long as wide at apex; postrostrum dorsally straight, squamose, similarly punctate as on head; prorostrum rather strongly declivous, more finely punctate than elsewhere, genae with some hairs besides a seta. Scape reaching middle of eyes; club 3.5x longer than wide, terminal segment 0.75x as long as other two segments together. Prothorax 1.13x wider than long, subparallel, with straight sides and laterally distinct apical collar; pronotum nearly straight in lateral view, distinctly convex transversely, with irregularly coarse puncta. Scutellum covered in fine piliform scales. Elytra triangular, at shoulders 1.80x wider than prothorax, 1.25x longer than own combined width, strongly tapering in straight line to apical one-quarter, then curving in to a rounded off apex; posthumeral knob much less laterally protruding than humeral callus. Striae well marked, here and there deviated by tubercles, puncta deep, centered with a slightly elongate scale; interstriae flat, 1, 3 and 5 with tubercles, on 1 (suture) three low, black or brown tufted tubercles behind middle, on interstria 3 with three tufted tubercles, a large and high one on middle, a small tubercle on the basal one-seventh and one not far behind the large tubercle. On interstria 5 are 2–3 low tubercles, apart from a preapical callus, of which the first tufted, situated a little further back than that on interstria 3. Fore coxae separated by more than width of antennal club. Metasternum between middle and hind coxae strongly convex. Femora with some alternating bare and squamose rings; tibiae strongly curved, adorned usually somewhat obliquely with dark bare and pale squamose rings, and roughed with large teeth on lower edge, the teeth smaller than mucro and premucro.

Length 6.5–8.7 mm.

REMARKS — *P. kanalensis* has the following combination of characters: highly prominent shoulders, widely separate fore coxae, a large tubercle on the middle of interstria 3 and curved tibiae with strong teeth on lower edge. Perroud described the species in remarkable detail. The adults cling to cloth and hands so firmly that are hard to shake or pick off. 69 species of *Syzygium* are listed as native for New Caledonia by Jaffré *et al.* (2001) but the only known host so far of *P. kanalensis* is *S. cumini*, an Australian species.

***Pterogonius millei* n. sp.**

Figure 23

TYPE MATERIAL — Holotype male: New Caledonia, 5.6 x 2.6 mm, Manjélia (Ouégoa), 20°23'S 64°33'E, 6 males, 2 females, 8 Feb 2005, on Myrtaceae, S Cazères & C Mille, in MNHN, Paris. Paratypes: 118 specimens in ANIC, BPBM, IRSN, MNHN, MNHW, NZAC, SRFP. New Caledonia: Mandjélia, lower creek, 20°24'S 164°32'E, 580, 1 male, 3 females, 12-13 Dec 2004, M Wanat; Mandjélia, summit, 780 m, 1 male, 4 females, 13 Dec 2004, M Wanat; Manjélia (Ouégoa), 20°23'S 64°33'E, 5 males, 2 females, 8 Feb 2005, on Myrtaceae, S Cazères & C Mille; Mandjélia, 700-750 m, 2 males, 11 Jan 2007, M Wanat; Mt Mandjélia, 700-780 m, 5 males, 6 females, 20-21 Nov 2008, M Wanat; Roches de la Ouaième, 3 females, 1 Nov. 2010, C. Mille; Pic d'Amoa, 360 m, 1 male, 14 Jan 2007, M Wanat & R Dobosz; Aoupinié, lower east road, 21°11'S 165°17'E, 600-800 m, 4 males, 5 females, 9 Feb 2004, M Wanat; Aoupinié, lower east road, 21°09'S 165°19'E, 500 m, 1 male, 17 Dec 2004, G Monteith; Aoupinié, 730 m, 1 pair, 7 Jan 2007, M Wanat & R Dobosz; Col d'Amieu, 450-470 m, 6 males, 6 females, 5-6 Jan 2007, M Wanat; Col d'Amieu, 450 m, 1 female, 15 Nov 2008, M Wanat; Farino, Parc des Grandes Fougères, 600-670 m, 3 males, 1 female, 17 Nov 2008, M Wanat; Mt Do, 800-920 m, 5-6 Nov 2008, M Wanat; Pic Ningua, -21.73965/166.15644, 1000 m, 5 Nov 2008, M Wanat ZUMAC Rd, junction, 22°02'S 166°28'E, 1 female, 9 Nov 2002, S Wright; Zumac Mts, 900 m, 13 males, 7 females, 28-29 Oct 2008, M Wanat & R Dobosz; Mt Koghi, 500-700m, 2 males, 28 Jan 1963, G Kuschel; Mt Koghis, 22°11'S 166°01'E, 700 m, 1 female, 3 Nov 2002, Burwell, Monteith, Wright; Haute Rivière Bleue, La Tranchée-Sentier des Kaoris, 22°05'S 166°38'E, 180-330 m, 4 specimens, 22-23 Jan 2004, M Wanat; same locality at 280-330 m, 8 specimens, 24 Jan 2004, M Wanat; Rivière Bleue Park, Grand Kaori, 22°06'S 166°41'E, 160 m, 2 specimens, 26 Jan 2004, M Wanat; Rivière Bleue, 190-339 m, 1 male, 20 Dec 2006, M Wanat & R Dobosz; Rivière Bleue, 330-560 m, 4 males, 4 females, 21 Dec 2006, M Wanat.

HOSTPLANT — Myrtaceae, eight specimens from Mandjélia were beaten off a myrtaceous species.

ETYMOLOGY — The species is named after Christian Mille in recognition for generous and friendly assistance to the author in the field, and making the collections of the Station de Recherches Fruitières de Pocquereux available for study.

DESCRIPTION — Black or piceous, antennae reddish brown. Vestiture squamose, faintly variegated, larger paler scales on part of pronotum, top of shoulders, sides of elytra below humeral callus, posthumeral knob and side of interstria 9 behind knob glabrous and shiny; underside with long lineal white scales and broader greyish brown scales on pleurites; femora and tibiae with long, semierect, squamiform setae. Head shiny, with moderately large puncta, with hairs and narrow scales; eyes weakly convex, symmetrical in dorsal view; forehead 0.72-0.84x as wide as rostrum at apex, shallowly depressed, frontal fovea present or absent. Rostrum 1.12-1.14x as long as prothorax, 2.54x longer than own width at apex; postrostrum occasionally with distinct median carina, squamose; prorostrum flat, finely punctate, genae glabrous except for a seta or two. Scape passing front margin but not reaching middle of eyes; club 2.95 times as long as wide, terminal segment 0.56 time as long as other two segments together. Prothorax 1.09 times wider than long, parallel-sided to apical third or quarter, with slight constriction at apex for a collar, disc weakly convex, with smooth median line on apical half, with a depression on either side of middle, coarsely, subrugosely punctate, larger scales on apical half and sides directed transversely, smaller ones on basal half directed obliquely forward. Scutellum black, very finely punctate and fine piliform scales. Elytra across posthumeral knobs 1.56-1.58x wider than prothorax, 1.51-1.56x as long as own width, gently converging to apical third;

striae with irregularly spaced deep puncta, these considerably larger than on pronotum; odd interstriae (1, 3, 5) with low tubercles often topped by short pale tufts, outer side of interstria 9 on middle section bare and shiny. Fore coxae contiguous; tibiae slightly curved, finely and sparsely denticulate on lower edge, with few long curved setae on sides. Male. Aedeagus in situ tilted to the right, asymmetrical at apex, slightly longer than venter; pedon nearly 1.4x as long as apodemes, well pigmented but somewhat translucent, parallel-sided to apical third, then asymmetrically attenuated to a blunt point at apex; in lateral view largely straight, curved down below ostium, then straighten out again; apodemes pale at apex; internal sac exposed between apodemes for half their length, with an inverted U-shaped sclerite near ostium and a large sclerite inside the exposed part, this sclerite robust, nearly as wide as pedon, extended at all four corners the anterior ones extending to the base itself of internal sac; ejaculatory duct insertion dorsal, entering basal sclerite at the anterior central area.

Length 5.4–7.1 mm.

REMARKS — This widespread and common species has at the midway area of the 9th interstria a conspicuously shiny glabrous area, tubercles on the elytral dorsum, weakly protruding, evenly convex eyes, and a metasternum between middle and hind coxae that is longer than a mid-coxal diameter.

Pterogonius sylviae n. sp.

Figure 24

TYPE MATERIAL — Holotype male: New Caledonia, 6.6x3.3 mm, Aoupinié, 21 Nov 2008, M Wanat, in MNHN. Paratypes: eight specimens in MNHW, NZAC, QMBA, SRFP. New Caledonia: Nehoué, camp ground, 20°25'S 164°13'E, 10 m, 1 male, 2 females, 9 Dec 2004, G Monteith; Pic d'Amoa, north slope, 20°58'S 165°17'E, 480 m, 1 female, 3 Jan 2005, G Monteith; Aoupinié, 21°17'S 165°30'E, 700 m, 2 males, 27 Nov 2008, M Wanat; Thio/route à l'heure, 21°35'S 165°09'E, 16 m, 1 female, 4 May 2006, S Cazères; Koghi Mts, 22°18'S 165°50'E, 340 m, 1 male, 25 Oct 2008, M Wanat.

HOSTPLANT — Unknown.

ETYMOLOGY — Named after the discoverer of the species Sylvie Cazères, assiduous collector of insects and assistant manager of collections at the Pocquereux Research Centre of La Foa.

DESCRIPTION — Integument largely shiny black, tibiae and tarsi dark reddish brown, antennae slightly paler. Vestiture on dorsum and pleurites with elongate ochrous scales mixed with white scales on pronotum and elytra, leaving most of striae bare, especially at base and on declivity; metasternum and venter with white lineal scales and some squamiform setae, sides and underside of femora and tibiae with white lineal scales and long, squamiform setae. Head with moderately large puncta, with large truncate scales not entirely concealing integument, leaving above frontal fovea a broad, glabrous line. Eyes rather strongly convex. Rostrum in male 1.22x shorter than prothorax and 2.48x longer than wide at apex, in female 1.16x shorter than prothorax and 2.92x longer than wide at apex, weakly curved, with a low, shiny and bare carina on midline and with ochrous scales from shortly behind antennal insertions to base; pronotum very finely punctate, glabrous on sides except for long genal seta. Scape not quite extending to middle of eyes; club 4x as long as wide, with dense, fine, semierect pubescence, 0.33x as long as other two segments together. Prothorax 1.0–1.12x wider than long, subparallel to middle, with laterally distinct apical collar, moderately convex, slightly impressed behind middle on either side, with a submarginal and median ochrous stripe, with sparser white scales on either side of midline from basal one-third to apical collar. Scutellum with narrow ochrous scales.

Elytra at laterally strongly protruding posthumeral knobs 1.65–1.70x as wide as prothorax, 1.4–1.5x longer than wide, rather strongly convex in lateral view; striae conspicuous with intermittent shiny wide stretches between striae 1 and 5, a narrow band just off one at base, an oblique band on basal one-third, another oblique one from stria 1 to 8 starting

at middle; glabrous and shiny below humeral callus and on sides of interstria 9; interstriae lacking tubercles on dorsal surface, with or without a low preapical callus. Fore coxae contiguous. Tibiae curved, robust, with well developed mucro and premucro, distinctly denticulate on lower edge.

Length 5.7-7.0 mm.

REMARKS — A distinctive species on account of broad habitus, abundant ochrous and white scales, broad, irregular, shiny striae, even interstriae without tubercles and without a distinct preapical callus.

22



23



24



25



FIGURES 22-25

22, *P. kanalensis*, male, 7.0 mm, Pocquereux (La Foa); **23**, *P. millei*, paratype male, 5.6 mm, Mandjélia; **24**, *P. sylviae*, paratype female, 6.8 mm, Thio/route; **25**, *P. tabularis*, holotype female, 5.1 mm. Table Unio. Scale bars = 1 mm.

***Pterogonius tabularis* n. sp.**

Figure 25

TYPE MATERIAL — Holotype female: New Caledonia, 5.1 x 2.3 mm, Table Unio, 21°34'S 165°46'E, 550-1000 m, 16 Oct 1978, JC Watt, in NZAC. Paratype: 1 female, same information as holotype, in NZAC.

HOSTPLANT — Unknown.

ETYMOLOGY — The specific name *tabularis* is an adjective from the Latin noun *tabula* for table in the sense of tableland.

DESCRIPTION — Integument reddish or yellowish brown. Scaly vestiture narrow or piliform on grey, yellow, reddish or brown areas, a stripe of larger white scales on either side of pronotum extended onto base of interstriae 5 and 6; underside mostly with long lineal white scales. Head with dense, moderately coarse puncta, with yellow or white piliform scales. Eyes moderately convex. Forehead 0.80x as wide as rostrum at apex, punctuation similar with that on head, scales wider and denser against eyes; fovea absent. Rostrum 1.14x shorter than prothorax, 2.1x longer than wide at apex; postrostrum on basal half as coarsely punctate as on head, with low median carina, ecales sparser and narrower than on forehead; prorostrum in lateral view weakly declivous, minutely punctate, punctuation of considerably lesser diameter than ommatidia, genae glabrous except for a seta. Antennae not quite reaching middle of eyes; club 3.2 longer than wide, terminal segment 0.75x as long as other two segments together. Prothorax 1.16x wider than long, subparallel, collar laterally distinctly marked, disc longitudinally flat, transversely convex, as densely and coarsely punctate as on head; apical margin behind eyes curving slightly forward. Scutellum with appressed white pubescence. Elytra at shoulders 1.55x wider than prothorax, 1.70x longer than their own combined width, moderately converging in straight line towards apical one-third, in lateral view moderately convex on dorsum; posthumeral knobs very low, rather indistinct, not at all showing on sides in dorsal view. Striae much narrower than interstriae, stria 9 from behind posthumeral knob and stria 10 alongside metepisternum considerably wider; interstriae lacking tubercles, interstria 5 with distinct preapical callus. Fore coxae contiguous. Metasternum in lateral view weakly convex. Femora slender, weakly clavate, lacking on lateral faces semierect setae; all tibiae lacking premucro, hind ones lacking also mucro.

Length 5.0-5.1 mm.

REMARKS — *P. tabularis* is distinguished by the presence of contiguous fore coxae, weakly clavate femora and indistinct posthumeral callus, and the absence of tubercles on elytra (apart from a preapical callus), and absence of a mucro on hind tibiae as well as absence of a premucro from all tibiae.

***Pterogonius tardus* n. sp.**

Figure 26

TYPE MATERIAL — Holotype male: New Caledonia, 7.1x3.5 mm, Mt Humboldt, 21°53'S 166°24'E, 1400 m, 2 males, 6 Nov 2002, Burwell, Monteith & White, in QMBA. Paratype: 1 male, same information as holotype, in NZAC.

HOSTPLANT — Unknown. Specimens collected at night in moss forest.

ETYMOLOGY — The epithet *tardus* is Latin for slow, clumsy because of flightless.

DESCRIPTION — Integument piceous, antennae and tarsi reddish brown. Vestiture squamose, with small, elongate, mostly lineal or piliform scales, these concentrated to form a loose stripe towards sides of pronotum, a dot on shoulders

and on posthumeral knobs and a white ring on hind femora. Head coarsely punctate, with puncta as coarse as on collar of pronotum and with lineal scales. Eyes weakly convex. Forehead 0.65x width of rostrum at apex, flat, with lineal scales, puncta a little less coarse than on head. Rostrum 1.2-1.3x shorter than prothorax, 2.13-2.23x longer than wide at apex, proximal half as coarsely punctate as head, covered in scales, without distinct carinae or rugae, distal half glabrous, becoming gradually finer, punctation very fine on prorostrum; genae lacking scales. Antennae slender, all segments of funicle longer than wide; scape extending to middle of eyes, moderately curved outwards; club 3.7x longer than wide, first two segments of same length, last one longer. Prothorax 1.09x wider than long, rounded on sides, widest at apical third, weakly constricted to a collar on sides, longitudinally more strongly convex than usual, disc much more coarsely punctate than collar, with narrow, rugose intervals. Scutellum small, round, finely punctate, lacking vestiture. Elytra across posthumeral knobs 1.32-1.34 wider than prothorax, 1.37-1.38x longer than own width, parallel-sided beyond lateral knobs, broadly rounded at apex, in lateral view flat on basal half, with a transverse depression on either side of basal quarter. Striae on basal half variable, narrower or wider than interstriae, tubercles on 1, 3, 5, 7, on 1 (sutural) with a tufted one near top of declivity, interstria 3 with two tubercles, one on middle, other on top of declivity, 3 with two tubercles, one on middle, other at top of declivity, interstria 5 with two tubercles plus a low, not tufted preapical callus, and interstria 7 with two tubercles as well; interstria 9 shiny, smooth, glabrous. Wings reduced. Underside with long, pili-form white scales; mesosternal process vertical in front; metasternum between middle and hind coxae distinctly shorter than a mid-coxal diameter, laterally impressed at first, then strongly convex, falling vertically against hind coxae. Femora strongly clavate, tibiae incurved at apex, finely denticulate, with small mucro, without premucro.

Length 6.5-7.1 mm.

REMARKS — *P. tardus* is the only flightless species amongst the dozen present. It is easily recognised by its deep body, rounded prothorax, small scutellum, parallel-sided elytra, pronounced elytral declivity and a strongly abbreviated metasternum.

Pterogonius vitiensis n. sp.

Figure 27

TYPE MATERIAL — Holotype not sexed: Fiji, 5.0 x 2.6 mm, Viti Levu: Lami [17°56'S 178°24'E], 0-700m, Feb 1977, NLH Krauss, in BPBM. Paratypes, 3 specimens not sexed, same information as holotype, in ANIC, NZAC.

HOSTPLANT — Unknown.

ETYMOLOGY — The epithet *vitiensis* is of Viti, the main island of Fiji.

DESCRIPTION — Integument piceous, femora and tibiae piceous or green, antennae and tarsi reddish brown. Vestiture squamose, scales narrow, lanceolate, lineal and piliform, not overlapping, larger on pronotum and sides of elytra and metasternum, forming on dorsal surface vague greyish, yellowish and brownish patterns; legs profusely squamose with broad scales; at least tubercle on middle of interstria 3 tufted. Head densely, coarsely punctate, with oblong scales. Eyes moderately protruding. Forehead narrow, 0.27x as wide as rostral at apex, densely squamose, lacking distinct fovea. Rostrum 1.15-1.22x shorter than prothorax, 2.2x longer than wide at apex, gently curved; postrostrum as coarsely punctate as head, with puncta regularly aligned, most of them confluent in grooves, finely carinate between contiguous grooves, basal half squamose; area between antennal insertions smooth, polished; prorostrum finely punctate, punctation much finer than ommatidia, genae lacking scales. Scape passing front margin but not reaching middle of eyes; club 2.7x longer than wide, terminal segment not longer than middle one. Prothorax 1.13-1.21x wider than long, subparallel, with slightly irregular sides, with margin behind eyes slightly curved; apical collar also dorsally distinct, disc flat, with a pair of small

bosses on either side of midline behind collar; punctation dense, coarse. Scutellum with fine greyish scales. Elytra across posthumeral knobs 1.53–1.63x wider than prothorax and $1.40=1.42$ x longer than own width 1.38x, widening considerably from humeral callus to posthumeral knob, then tapering towards apical one-third and curving onto apex. Striae much narrower than interstriae, stria 9 distinctly sulcate and wider; interstria 3 with three tubercles, lowest on basal one/seventh, largest on middle topped with a tuft of ochrous and black setiform scales, a 3rd one on top of declivity, interstria 5 with a small tubercle slightly behind middle, and a low but distinct preapical callus, interstria 9 neither compressed nor shiny alongside stria 10. Fore coxae contiguous. Metasternum between middle and hind coxae moderately convex. Femora strongly clavate; tibiae curved, coarsely dentate, the teeth smaller than mucro and premucro.

Length 5.0–5.4 mm.

REMARKS — *P. vitiensis* is readily separated from all other species by its very narrow forehead and a strikingly flat pronotum.

Pterogonius wanati n. sp.

Figure 28

TYPE MATERIAL — Holotype (not sexed): New Caledonia, 4.4x2.0 mm, Tiéa [Tiaoué] Forest (GIE Fab Nicoli), 21°07'S 164°57'E, 30 m, in MNHN, Paris. Paratypes: 5 specimens (not sexed), in MNHW, NZAC, 30 Jan 2004, M Wanat.

HOSTPLANT — Unknown; adult specimens beaten in sclerophyll forest.

ETYMOLOGY — The species is named after Dr Marek Wanat, specialist in the study of apionids and sedulous collector of beetles.



FIGURES 26–28

26, *Pterogonius tardus*, holotype male, 7.1 mm, Mt Humboldt; 27, *P. vitiensis*, holotype, 5.0 mm, Viti Levu; 28, *P. wanati*, paratype, 4.0 mm, Tiéa Forest. Scale bars = 1 mm.

DESCRIPTION — Integument dark or reddish brown, elytra mostly darkened at base of interstriae 1-5. Vestiture squamose, rather dense, nearly concealing integument on elytra. Head densely, coarsely punctate, with piliform and elongate scales. Eyes moderately convex. Forehead 0.75 of rostrum width, scales elongate-elliptic and denser against eyes. Rostrum 1.47x shorter than prothorax, 1.70x longer than wide at apex, coarsely, densely punctate, without carina or rugae, with scales on basal half similar to those on forehead; pronotum twice as wide as long, gradually more finely punctate towards apex; genae with lineal and piliform scales. Scape extending to middle of eyes; 1st segment of funicle 1.3x longer than 2nd; club 3x longer than wide, segments of same length or last one a fraction longer. Prothorax 1.04x wider than long, parallel-sided on basal two thirds, gently constricted to a weak broad collar, longitudinally and transversely moderately convex, densely punctate, scaling moderately dense, variable in size and distribution, usually longer on sides. Scutellum covered in piliform white scales. Elytra 1.58x wider than prothorax, 1.52x longer than own maximum width, slightly widening towards posthumeral knob, then gently tapering to apical third before converging, ending with two short sutural tufts (points). Striae variable in width from as wide as or wider than interstriae to distinctly narrower; interstria 3 with three low tubercles, one or more of them topped with short tufts, interstria 5 with a prominent, tufted preapical callus, interstria 9 on middle area squamose, not glabrous or particularly shiny. Tibiae finely asperate or denticulate on lower edge, incurved at apex, with small mucro and premucro.

Length 3.9-4.8 mm.

REMARKS — There are no salient features distinguishing this species apart from those in the key.

ACKNOWLEDGMENTS

For the loan of specimens I wish to thank R. Leschen (Landcare Research, Auckland), K. Desender and P. Grootaert (Institut Royal des Sciences Naturelles de Belgique, Brussels), C. Mille and S. Cazères (Station de Recherches Fruitières de Pocquereux, La Foa), M. Wanat (Museum of Natural History, Wrocław), G. Monteith (Queensland Museum, Brisbane), R. Oberprieler (Division of Entomology, CSIRO, Canberra) and G. A. Samuelson (Bernice P. Bishop Museum, Honolulu). For the digital images, their numbering and arrangement into sets of figures I am indebted to B. Rhode (Landcare Research, Auckland) and last, not least, P. Grandcolas (Muséum national d'Histoire naturelle, Paris) for editing this and the other papers accepted for publication in *Zoologia Neocaledonica*.

REFERENCES

-
- FAUST J. 1889 — Beitrag zur Käferfauna zweier Inseln. *Stettiner Entomologische Zeitung* 50 (1-3): 61-106.
- GEMMINGER M. & HAROLD E. VON 1871 — Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus, Curculionidae. Monachii, E. H. Gummi (G. Beck), vol. 8: 2181-2668 + 10 + 1 p.
- KUSCHEL G. 2008 — Curculionoidea (weevils) of New Caledonia and Vanuatu: Basal families and some Curculionidae, in GRANDCOLAS P. (ed.), *Zoologia Neocaledonica* 6, *Mémoires du Muséum national d'Histoire naturelle* 197: 99-249.
- JAFFRÉ T., MORAT P., VEILLON J.-M., RIGAUULT F. & DAGOSTINI G. 2001 — Composition et caractérisation de la flore indigène de Nouvelle-Calédonie. *Techniques*, IRD II (4): 1-121.
- MONTROUZIER X. 1861 — Essai sur la faune entomologique de la Nouvelle-Calédonie (Balade) et des îles des Pins, Art, Lifu, etc. *Annales de la Société Entomologique de France* (3) 8 (4): 867-916 [1860].
- OBERPRIELER R. G. 2010 — A reclassification of the weevil subfamily Cyclominiinae (Coleoptera: Curculionidae). *Zootaxa* 2515: 1-35.
- RISBEC J. 1936 — Les parasites du caféier en Nouvelle-Calédonie. *L'Agronomie coloniale* 25 (226): 105-123.
- RISBEC J. 1942 — Observations sur les insectes des plantations en Nouvelle-Calédonie. Paris, Direction des Affaires Économiques, Section technique d'Agriculture tropicale, pp. 78-83.

APPENDIX 1

Notes on homonymy and synonymy in Molytini (Coleoptera: Curculionidae).

The writing of mine on the *Orthorhinus* genus-group of Molytini in *Zoologia Neocaledonica* 6 requires some corrections. I am grateful to Miguel Alonso-Zarazaga for drawing attention to a homonymy that arose by the same name *Faustius* having been proposed by two authors. I wish to thank Christian Mille for sending copies of two papers of J. Risbec, one published in 1936 describing *Coffearhynchus* without inclusion of illustrations, the other in 1942 reproducing the same description but with the addition of two figures. I also want to express my sincere thanks to Hélène Perrin for providing excellent photos of the head, prothorax and legs, as well of the labels attached to the holotype, of *Coffearhynchus neocaledonicus* Risbec deposited in the Muséum national d'Histoire naturelle, which allowed me to establish its synonymy with a species of Montrouzier.

The corrections are:

Coffearhynchus Risbec, 1936: 112 (type species *C. neocaledonicus* Risbec, 1936).

Orthorhinoides Kuschel, 2008: 204 (type species: *Orthorhinus cylindricus* Montrouzier, 1861) n. syn.

Coffearhynchus cylindricus (Montrouzier, 1861) n. comb. (from *Orthorhinoides*).

Coffearhynchus neocaledonicus Risbec, 1936: 113 n. syn. - Risbec 1942: 78, fig. 95, 96.

Faustiellus n. nom. for *Faustius* Kuschel, 2008 (non Arzanov 2006).

APPENDIX 2

More materials of the groups of New Caledonian weevils dealt with in my last publication (2008) have turned up. One is of special interest and described below in the genus *Amphionotus*.

Amphionotus undulatus n. sp.

Figures 29, 30

TYPE MATERIAL — Holotype male: New Caledonia, 14.2-15.8 mm, Haute Rivière Bleue, 22°05'S 166°38'E, 280-330 m, 24 Jan 2004, M Wanat, in MNHN, Paris. Paratypes: Pic du Pin, 22°15'S 166°49'E, 280 m, 1 male, 26 Nov 2004, Queensland Museum Party, in QMBA.

HOSTPLANT — Unknown; beaten from rainforest mixed vegetation.

ETYMOLOGY — The species name is a Latin epithet meaning wavy, from undulae for small waves.

DESCRIPTION — Integument black. Vestiture squamose, scales small, ovate, grey, partly metallic pink, uniformly spread, not completely covering derm, finer or absent on transverse rugae of pronotum and elytra.

Head not or inconspicuously constricted behind eyes, very finely punctate under scaling. Rostrum with high, strong, shiny carina on midline flanked by deep, broad, squamose groove, dorsal margin on sides shiny, finely punctate. Epistome distinctly raised, large, triangular, flat, bordered by piliform scales, with a tuft of three short, robust, brown vibrissae; hairs on mandibles similar to the epistomal vibrissae, fewer and shorter than in *A. douei*; underside medially very shiny, without setae, with a deep groove on either side; prementum completely alutaceously dull, without setae. Scrobes deeply sulcate, at most sparsely squamose. Scape gently curved, not extending beyond hind margin of eyes; segment 2 of funicle slightly longer than 1; club black.



FIGURES 29-30

Amphionotus undulatus, holotype male, 14.2 mm, Haute Rivière Bleue. Scale bars = 5 mm.

Prothorax 1.43x wider than long, slightly bisinuous at base, truncate at apex, widening in nearly straight line to apical third, then quickly narrowing to a distinct broad collar; disc medially flat lengthwise and across, with vague transverse waves or strong shiny rugae. Scutellum distinctly exposed, level with elytra.

Elytra at shoulders 1.20x, at widest part 1.38x wider than prothorax, twice as long as wide across shoulders, distinctly sinuous at base, with small, prominent humeral callus and a smaller and lower tubercle on interstria 7 beyond middle at 0.55 of elytral length; suture extended by a double parallel knob beyond abdomen; striae fine; dorsal surface with transverse waves or rugae.

Metasternum distinctly shorter than a mid-coxal diameter; ventrites shallowly impressed, medially pubescent. Femora weakly clavate, fore and middle tibiae with well developed mucro and denticulate on lower edge, hind tibiae not denticulate, lacking mucro.

REMARKS — The main characters separating *A. undulatus* from *A. douei* are: presence of a high median carina on the rostrum flanked by a deep broad groove, a scape curved and not passing hind margin of eyes, a pronotum without transverse impression, a distinctly well-exposed scutellum, a sinuous basal margin on elytra, and prothorax as well as elytra dorsally uneven with transverse waves or rugae.

The blind weevils of Myrtonymina in New Caledonia and Australia (Curculionidae: Curculioninae: Eirrhiniini: Myrtonymina)

Guillermo Kuschel

7 Tropicana Drive - Mt Roskill - Auckland 1041 - New Zealand
g.kuschel@xtra.co.nz

ABSTRACT

A subterranean weevil recently discovered in New Caledonia prompts a study of the Myrtonymina group of Eirrhiniini. The subtribe Myrtonymina is the southern hemisphere counterpart of the northern hemisphere Raymondionymina, two groups that exhibit all the characters of Eirrhiniini except for their cryptic life at all stages in an underground habitat. They are small, depigmented, devoid of pubescence and scales, have erect sensory hairs, and are truly apterous and blind. The genitalic configuration is similar to that of basal families of Curculionoidea. This make-up is the sole feature separating Eirrhiniini from other tribes in the subfamily Curculioninae. Eirrhiniini are associated with a prodigious array of hostplants, extending from Bryophyta and Pteridophyta through to Dicotyledons and Monocotyledons but bypassing Gymnospermae. The circumstantial evidence points at the two blind hypogean groups to be feeding on roots of Dicotyledons, and the Australasian Myrtonymina hinting at an ecological association with Myrtaceae.

The new taxa are *Hexonymus reginalis* n. gen. and sp. from Queensland, and the new species *Myrtonymus caledonicus* from New Caledonia, *M. australicus* and *M. moorei* from New South Wales, *M. eucalypti* and *peckorum* from Western Australia.

RÉSUMÉ

Les charançons aveugles de Myrtonymina en Nouvelle-Calédonie et en Australie (Curculionidae : Curculioninae : Eirrhiniini : Myrtonymina).

Un charançon souterrain récemment découvert en Nouvelle-Calédonie invite à une étude du groupe Myrtonymina de Eirrhiniini. La sous-tribu Myrtonymina dans l'hémisphère Sud est la contrepartie de Raymondionymina dans l'hémisphère nord, deux groupes présentant tous les caractères des Eirrhiniini à l'exception de leur vie cryptique à toutes les étapes d'un habitat souterrain. Ils sont petits, dépigmentés, dépourvus de pilosité et d'écaillés, ont des poils sensoriels dressés et sont vraiment aptères et aveugles. La configuration génitale est similaire à celui des familles basales de Curculionoidea. Cette configuration est la seule caractéristique qui sépare les Eirrhiniini

des autres tribus dans la sous-famille des Curculioninae. Les Eirrhiniini sont associés à une gamme prodigieuse de plantes hôtes, s'étendant des Bryophytes et Ptéridophytes aux Dicotylédones et Monocotylédones mais en évitant les Gymnospermes. Il est proposé par déduction que les deux groupes hypogées aveugles se nourrissent par les racines des Dicotylédones et que les Myrtonymina sont associés écologiquement avec les Myrtaceae.

Les nouveaux taxons sont *Hexonymus reginalis* n. gen. et sp. du Queensland et les nouvelles espèces *Myrtonymus caledonicus* de Nouvelle-Calédonie, *M. australicus* et *M. moorei* de la Nouvelle-Galles du Sud, *M. eucalyptus* et *M. peckorum* d'Australie occidentale.

INTRODUCTION

The first species of Myrtonymina to be known was *Myrtonymus zelandicus* Kuschel, 1990 from New Zealand. It was discovered whilst surveying the beetle fauna of an estuary vegetation of Auckland. The minute, blind, well under a millimetre long weevil is considered related to the equally blind northern hemisphere Raymondionymina, and placed alongside in a subtribe of its own within the tribe Eirrhiniini, subfamily Curculioninae. It was known at the time of its description that the genus occurred in Australia as well but without a named species. Because a specimen of a new species of *Myrtonymus* recently turned up in New Caledonia, the opportunity of dealing with this species is seized to include descriptions of a new genus and five new species from Australia owing to their systematic and biogeographical interest and relevance.

HIERARCHICAL STATUS

Faunal elements living permanently underground are characterised by blindness, smallness, apterism, depigmentation, presence of erect sensory hairs and adaptive expressions of their fossorial live in friable soils. Such faunas invariably derive from cryptic forms adapted to rich bushfloor litter, or subaquatic and aquatic environs.

Raymondionymina and Myrtonymina, the two groups of anophthalmic weevils, together with those having normal eyes and much the same type of genitalia of basal families were initially brought together simply for convenience in a taxonomic, artificial, but practical subfamily Eirrhiniinae (Kuschel 1971). It was done in accordance with the then prevailing concept of the taxon. As a result of a subsequent phylogenetic analysis of the whole superfamily Curculionoidea, the subfamily status became demoted to a tribe within Curculioninae (Kuschel 1990, 1995). No explanation was given by the authors who recognized two groups with full family status, Eirrhinidae for all the ophthalmic forms living on and above the ground, and Raymondionymidae for the anophthalmic forms living below the ground in the soil (Ienistea 1986; Thompson 1992; Zimmerman 1993; Alonso-Zarazaga & Lyal 1999). It is not important how the taxa are currently perceived. Results from molecular sequencings will hopefully help one day in the not too far future to more accurately evaluate the real relationships between the weevil groups that seem to differ solely in sharing similar genitalic characters with basal families of Curculionoidea.

BIOLOGY AND ECOLOGY

Although the northern hemisphere Raymondionymina are known since the early 1860s, and much attention was given to this Holarctic component of fauna, information about their life and host associations is scarce and poor beyond the observations carried out on *Raymondionymus perrisi* Grenier by Remillet (1968), who came to the conclusion that this species can feed on several unrelated plants. There are 58 recognised species in 15 genera in Raymondionymina according to a detailed and profusely illustrated revision of the group by Osella (1977).

Eirrhiniini are largely associated with hosts from aquatic and subaquatic habitats, ranging from moss, horsetails and ferns to monocots and dicots but bypassing conifers and other gymnosperms. Some larvae of the tribe are endophytic and develop in the plant tissue, others are ectophytic and feed freely from the outside. It is still unknown whether these soil inhabiting blind weevils are associated with specific plants. Remillet (1968) after experimenting with *P. perrisi* found that this species can feed upon several unrelated plants. It might be assumed that a departure from a normal diet occurred for a flightless and blind phytophagous group living permanently in soil.

Out of the seven species of *Myrtonymina* now known, four were found at the base of stems and around roots of Myrtaceae growing in loose, friable soils. Their small size, slender body, strong and heavy tibial combs and broad, compact tarsi enables them to work their way easily through the loam. When the ground is rather wet they are near the surface, otherwise, particularly in periods of drought, deep down.

MATERIAL AND METHODS

All *Myrtonymina* specimens studied are less than a millimeter long, far too small to be collected with the naked eye in the field. There are two ways to secure specimens of endogean faunas, the washing and sifting soil method used by nematologists and the deep pit-trap method (Kuschel 1991, 1995). The washing of soil through sieves of progressively finer mesh is highly recommendable, as any sample will invariably contain also easily identifiable parts of bodies should species occur there. Preparations of whole bodies and parts on acetate plates are mandatory for proper study and identification.

Length of body is always measured by me from the middle of eyes to the end of body on a specimen in a normal and relaxed position unless otherwise stipulated. Blind species are measured by excluding the head.

Depositories.

ANIC: Australian National Insect Collection, CSIRO, Canberra, Australia.

MNH: Muséum national d'Histoire naturelle, Paris, France.

NZAC: New Zealand Arthropod Collection, Landcare Research, New Zealand.

SYSTEMATIC PART

Family CURCULIONIDAE Latreille, 1802

Subfamily CURCULIONINAE Latreille, 1802

Tribe ERIRHININI Schoenherr, 1825

Subtribe MYRTONYMINA Kuschel, 1990

Type genus. *Myrtonymus* Kuschel, 1990

DESCRIPTION — An Australasian hypogean group of under a millimetre long, blind, depigmented weevils with erect sensory hairs, defined as follows: Head and rostrum porrect, only slightly diverted downwards from axis of body, converging, in dorsal view, in straight line to insertion points of antennae, without any constriction or indentation between head and rostrum, and with a knobby expansion above antennal insertions, with erect hairs on postrostrum directed slightly backwards (caudad), on prorostrum directed forward (apicad); scrobes nearly foveiform, directed obliquely downwards, lacking secondary scrobes; scape extending as far as smooth part of head; funicle with 6 or 7 segments, segment 1 thicker and considerably longer than 2, remainder of segments moniliform or transverse, only slightly widening towards club; club elongate-oval. Prothorax longer than wide, with or without an apical constriction on sides, with an annular constriction at base, without postocular lobes, with nearly vertically descending front margin. Scutellum usually distinct. Elytra elongate-elliptic, at least twice as long as wide, ascending obliquely at base, lacking humeral callus, punctation fine, irregularly lined up to striae; wings absent. Prosternum neither emarginate nor canaliculate, at least twice longer than behind coxae; metasternum longer than a mid-coxal diameter. Ventrites 1 and 2 fused, with or without suture, ventrite 3 completely free from 2, 4 and 5 fused to a variable degree, at times obsolescent, with a low flange on floor of abdominal lumen. Front coxae contiguous or subcontiguous, middle coxae narrowly separate. Femora pedunculate, incrassate, unarmed, not sulcate underneath. Tibiae without a mucro or uncus, (apparently) with spurs, with combs and fringes much as illustrated for *Myrtonymus zelandicus* (Kuschel, 1990). Tegmen as long as aedeagus or a quarter shorter; strongly

stretched caudad in lateral view, dorsally large, with broad parameral lobes, these usually with a few setae; aedeagus as long as or longer than abdomen; pedon shorter than apodemes, tectum pigmented or clear; apodemes laterally inserted, without obvious articulation with pedon, with pedal and tectal arms; internal sac amply visible between apodemes, with flagellum or with a bulky, rigid structure as a basal sclerite.

REMARKS — Genera of the subfamily Curculioninae that have an aedeagus with similar characteristics to those of basal weevil families are being provisionally brought together into a likely paraphyletic tribe Erihrinini to draw attention to a highly plesiomorphic condition defining Raymondionymina and Myrtonymina.

KEY TO SPECIES OF MYRTONYMINA

1. Antennae with a 7-segmented funicle. Genus *Myrtonymus* 2
 - Antennae with a 6-segmented funicle. Length 0.85 mm Genus *Hexonymus* (*H. reginalis*)
- 2 Species from New Caledonia and New Zealand. Aedeagus with a rigid, relatively large basal sclerite 3
 - Species from Australia. Aedeagus with flagellum or rigid basal sclerite 4
- 3 Scutellum absent. Length 0.76 mm. New Caledonia *M. caledonicus*
 - Scutellum present. Length 0.70-0.82 mm. New Zealand *M. zelandicus*
- 4 Aedeagus with a bulky basal sclerite instead of a flagellum 5
 - Aedeagus with a flagellum instead of a bulky basal sclerite 6
- 5 Pale reddish-brown. Antennal scape weakly clavate. Male (Figure 22): parameral lobes narrow, broadly disjunct; pedon symmetrically rounded at apex. Length 0.77-0.82 mm *M. eucalypti*
 - Dark reddish-brown. Antennal scape strongly clavate. Male (Figure 23): parameral lobes broad, narrowly disjunct; pedon asymmetrically rounded at apex. Length 0.75-0.78 mm *M. peckorum*
- 6 Prothorax, in dorsal view, indistinctly constricted on sides at apex. Length 0.77-0.87 mm. Australia
 - *M. australicus*
 - Prothorax, in lateral view, distinctly constricted on sides at apex. Length 0.90-0.98 mm. Australia
 - *M. moorei*

Genus *MYRTONYMUS* Kuschel, 1990

Myrtonymus Kuschel, 1990: 80

Type species. *M. zelandicus* (Kuschel, 1990)

DESCRIPTION — Scape moderately widened at apical third; funicle 7-segmented; prothorax with or without an apical constriction on sides and distinctly larger punctation; erect hairs on entire dorsal surface relatively long.

DISTRIBUTION — New Zealand, New Caledonia, Australia.

HOSTPLANT — Unknown, but adults consistently associated with soil around rootlets of Myrtaceae.

ETYMOLOGY — *Myrtonymus* is a transliterated Greek word composed of *myrtos* = myrtle, and *ónyma* meaning word or designation.

***Myrtonymus caledonicus* n. sp.**

Figures 1, 2, 3

TYPE MATERIAL — Holotype male: New Caledonia, 0.75 x 0.28 mm, Mont Do (Boulouparis), 21°45'S 160°00'E, 928 m, 1 male, 22 Nov 2007, sol de sous-bois, T Théry, in MNHN, Paris.

ETYMOLOGY — *Caledonicus* refers to New Caledonia.

DESCRIPTION — Rostrum plus head 1.11 x shorter than prothorax, 2.50 x longer than wide across antennal insertions, punctation much finer than on pronotum; frontal fovea absent.

Prothorax 1.33 x longer than wide, with indistinct apical constriction on sides; punctation as coarse as on elytra. Scutellum absent. Elytra 1.43 x wider than prothorax, 1.83 x longer than at widest point, a little less shiny than pronotum, with slightly leather-like (coriaceous) dorsal surface.

Male. Aedeagus (Figures 2, 3) 210 μ by appr. 63 μ wide; pedon 1.20 x longer than wide, truncate, dorsal surface (tectal area) clear; internal sac with a pair of frenal sclerites (these briefly extruded in the slide) and a relatively bulky, curved, well pigmented tubular, 132 μ long basal sclerite with a short extension at base for reception of ejaculatory duct.

Length 0.75 mm.

REMARKS — The discovery of a *Myrtonymus* species at a relatively high altitude (928 m) in New Caledonia was somewhat unexpected.

***Myrtonymus zelandicus* Kuschel, 1990**

(Figures 4, 5, 6, 7)

Myrtonymus zelandicus Kuschel, 1990: 81, figs 106-116.

TYPE MATERIAL — Holotype male: New Zealand, 0.77 x 0.25 mm, Lynfield, 2 Aug 1975, G Kuschel, in NZAC, Auckland; paratypes in a number of national and overseas museums and institutions.

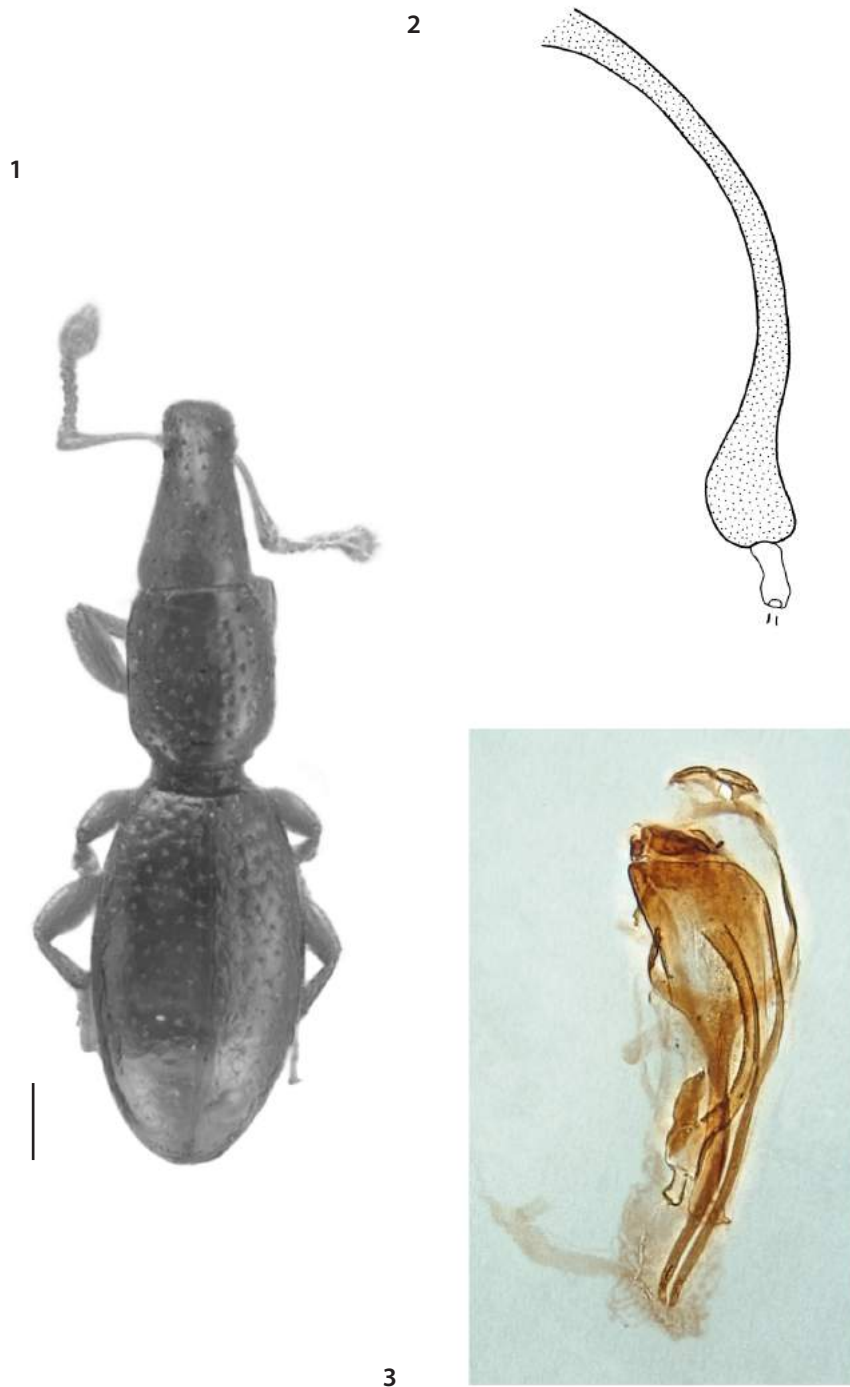
MATERIAL EXAMINED — New Zealand. North Island: east coast from Houhora in Northland to Auckland City, Poor Knights Islands and Little Barrier Island.

HOSTPLANT — Associated with the myrtaceous genera *Kunzea*, *Leptospermum*, *Lophomyrtus*, *Metrosideros*.

DESCRIPTION — **Male.** Aedeagus 196 μ long by appr. 59 μ wide; pedon 1.27 x longer than wide, truncate at apex; tectal area clear; apodemes about 1.78 x longer than pedon, without a bridge near base; internal sac with a pair of frenal sclerites and with a large, bulky, strongly curved, well pigmented, 118 μ long basal sclerite and separated from a weakly pigmented structure at gonopore area by a membranous section.

Length 0.70-0.82 mm.

REMARKS — The aedeagus of the species is 196 μ long by 59 μ wide; the solid, larger and more intensely pigmented part of the basal sclerite is 118 μ long (Figure 7), the lateral view of it in Figure 7 shows the difference from that in Figure 3 of *M. caledonicus*.



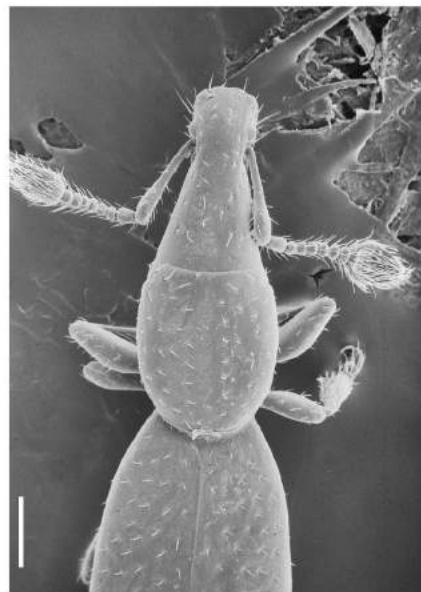
FIGURES 1-3

1, *Myrtonymus caledonicus* n. sp., Mont Do, New Caledonia, holotype male, 0.75 mm; **2**, aedeagus length (from tip of pedon to end of apodemes) 210 μ ; **3**, sclerite, length 132 μ .

4



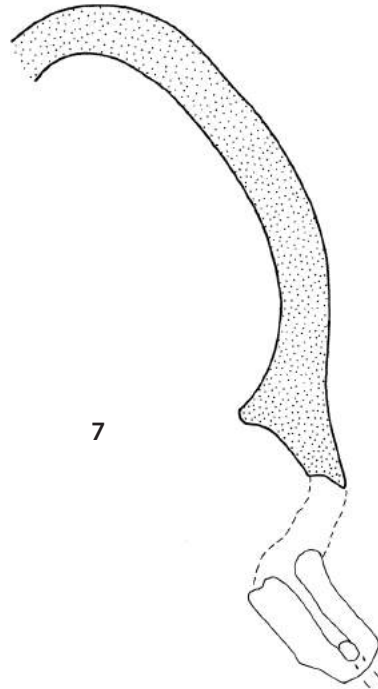
5



6



7

**FIGURES 4-7**

M. zelandicus, Lynfield, New Zealand, male: **4**, habitus, 0.72 mm; **5**, head and prothorax; **6**, aedeagus, length 196 μ ; **7**, sclerite, length 118 μ .

***Myrtonymus eucalypti* n. sp.**

(Figures 8-10)

TYPE MATERIAL — Holotype male: Australia, 0.81 x 0.24 mm, Western Australia, Suas Bridge, 50 km SW of Nannup, 1 male, 2 females, 26 Jul 1980, log litter of *Eucalyptus calophylla*, SB & J Peck, in ANIC, Canberra. Paratypes: 3 specimens in ANIC, NZAC. Suas Bridge, 50 km SW of Nannup, 2 females, 26 Jul 1980, log litter of *Eucalyptus calophylla*, SB & J Peck; Brockman N. P., Pemberton, 1 female, 9 Jul 1980, litter of *Eucalyptus diversicolor*, S & J Peck.

HOSTPLANT — Association with *Eucalyptus calophylla*, *E. diversicolor*.

ETYMOLOGY — The species name *eucalypti* is genitive case of *Eucalyptus* (Myrtaceae), to express association of this and other *Myrtonymus* species with the gum-tree genus *Eucalyptus*.

DESCRIPTION — Pale reddish-brown. Rostrum plus head as long as prothorax, 3.00-3.13x longer than wide across antennal insertions; head smooth; rostrum considerably more finely punctate than prothorax, not confluent; frontal fovea absent or minute; antennal scape weakly clavate at apex. Prothorax 1.27-1.40x as long as wide, with straight sides, a fraction wider towards apical third, in dorsal view with indistinct constriction on sides at apex; punctation sparse, considerably coarser than on elytra. Scutellum small. Elytra 1.15-1.33 x wider than prothorax and 2.10-2.50 x longer than own maximum width; dorsal surface not coriaceous, smooth between setiferous punctules; striae puncta variable in size and irregularly line up.

Femora strongly incrassate, distinctly pedunculate.

Male. Tegmen as long as aedeagus; parameral lobes disjunct, moderately wide, with apical seta. Aedeagus nearly symmetrical, 260 μ long; pedon nearly parallel-sided, 1.48 x longer than wide, broadly rounded at apex; apodemes 1.71 x longer than pedon, with weakly pigmented pedal arms and very faintly pigmented tectal arms.

Length 0.79-0.81 mm.

***Myrtonymus peckorum* n. sp.**

(Figures 11-13)

TYPE MATERIAL — Holotype male, Australia, 0.78 mm, WA, Normalup, Valley of Giants, 21 June 1980, S. & J. Peck // rotted bark, *Eucalyptus jacksonii*, SBP/WA74, in ANIC; paratypes in ANIC, NZAC.

MATERIAL EXAMINED — Australia, Western Australia, 3 specimens, Normalup, Valley of Giants, 21 June 1980, S. & J. Peck // rotted bark, *Eucalyptus jacksonii*, SBP/WA74.

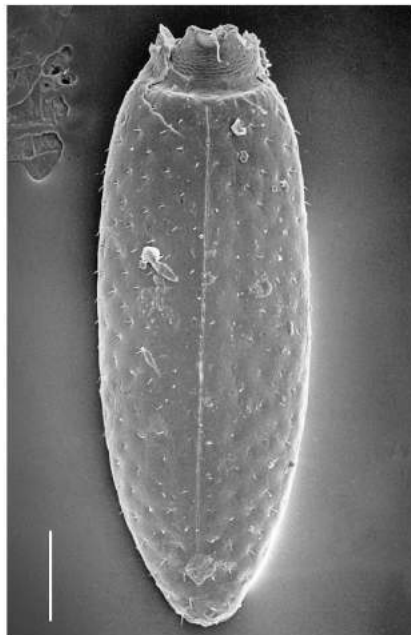
HOSTPLANT — Association Association with *Eucalyptus jacksonii*.

ETYMOLOGY — Species named after S.B. & J. Peck, who collected most of the specimens.

DESCRIPTION — Dark reddish-brown. Rostrum plus head slightly shorter than prothorax, 2.5-3.0 x longer than wide across antennal insertions; rostral punctation non-confluent, much finer than on prothorax; frontal fovea absent, if present then exceedingly small and distinctly finer than adjacent puncta; scape rather strongly clavate at apex. Prothorax 1.17-1.37 x as long as wide, with straight sides and rounded off apical and basal angles, without collar indentation on sides. Elytra 1.25-1.40 x wider than prothorax, 1.86-2.09 x longer than own maximum width, with fine, indistinctly lined up striae punctation.



8



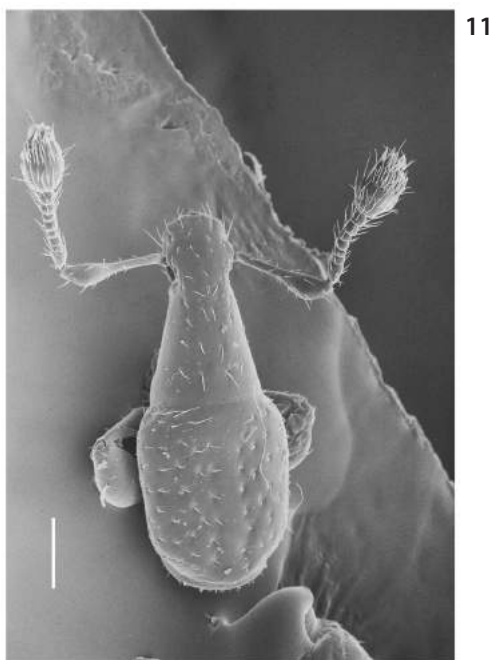
9



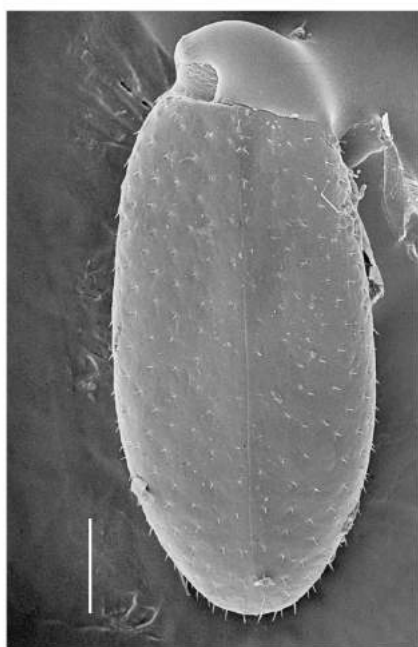
10

FIGURES 8-10

M. eucalypti n. sp., Suas Bridge, Western Australia, male, 0.78 mm: **8**, head and prothorax; **9**, elytra; **10**, aedeagus, length 260 μ .



11



12



13

FIGURES 11-13

M. peckorum n. sp., Normalup, Western Australia, male, 0.87 mm: **11**, head and prothorax; **12**, elytra; **13**, aedeagus, length 250 μ .



14



15



16



17



18

FIGURES 14-18

M. australicus n. sp. nr Bonville, N.S. W., Australia, female, 0.80 mm: **14**, habitus; **15**, head and prothorax; **16**, middle tibia and tarsus; **17**, hind tibia and tarsus; **18**, aedeagus, length 289 μ .

Male. Tegmen as long as aedeagus; parameral lobes narrowly disjunct, wide, broadly rounded at apex. Aedeagus asymmetrical, 250 μ long; pedon approximately 1.5 x longer than wide, gently rounded on sides, broadly, obliquely rounded at apex; apodemes 1.7 x longer than pedon, with weakly pigmented pedal arm and a nearly clear tectal arm; internal sac extended to end of apodemes, with flat, irregularly shaped blade-like sclerites inside aedeagal body and between basal area of apodemes, and a somewhat S-shaped basal sclerite similar with that of *M. eucalypti* but smaller and narrower.

Length 0.79-0.80 mm.

***Myrtonymus australicus* n. sp.**

(Figures 14-18)

TYPE MATERIAL — Holotype female: Australia, 0.87 x 0.31 mm, 8 km W of Bonville [30°22'S 153°02'E], 9 Dec 1967, RS McInnes, in ANIC. Paratypes: same information as holotype, 2 males, 3 females, in ANIC, NZAC.

HOSTPLANT — Unknown.

ETYMOLOGY — *Australicus* is Latin for one of the variants of Australian.

DESCRIPTION — Rostrum 0.97-1.06 x as long as prothorax, 2.60-2.80 x longer than wide across at antennal insertion knobs; punctuation much finer than on pronotum, largely confluent, forming fine longitudinal lines or folds; frontal fovea absent. Prothorax 1.25-1.31 x longer than wide, weakly rounded or straight on sides, apical constriction rather indistinct, punctuation slightly coarser than on elytra. Scutellum very small. Elytra 1.23-1.27 x wider than prothorax, 2.03-2.11 x longer than wide at maximum width, dorsally not coriaceous at 50x magnification. Femora weakly incrassate, with short, rather indistinct peduncle.

Male. Aedeagus 289 μ long by 78 μ wide; internal sac with a 402 μ long flagellum 1.39 x longer than aedeagus including apodemes.

Length 0.77-0.87 mm.

***Myrtonymus moorei* n. sp.**

(Figures 19- 23)

TYPE MATERIAL — Holotype male: Australia, 0.975 x 0.355 mm, New South Wales, Shingle Hill, near Gundaroo, 33 km N of Canberra, 15 Feb 1981, BP Moore, in ANIC, Canberra. Paratypes: 15 males, 14 females, same locality as holotype, 25 Jun 1971 and 15 Feb 1981, BP Moore; 1 pair, 15 Oct 1979, ex litter and top 4 cm humus samples 79/114 and 79/115, G Kuschel, in ANIC, NZAC.

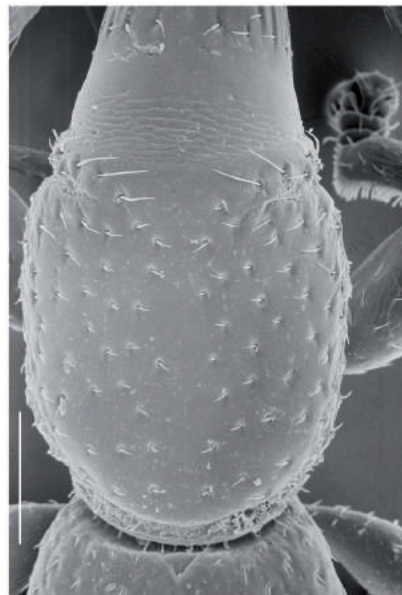
HOSTPLANT — *Eucalyptus macrorhyncha* (Myrtaceae).

ETYMOLOGY — Species named after Dr Barry P. Moore, CSIRO, Canberra, who discovered the species and collected a nice series of specimens.

DESCRIPTION — Rostrum 1.1-1.3 x shorter than prothorax, 2.3-2.6 x longer than wide across antennal insertions; punctuation finer than on prothorax, largely confluent forming longitudinal streaks; frontal fovea distinct, usually sulci-form, relatively large. Prothorax 1.20-1.25 x longer than wide, parallel-sided or gently rounded, in dorsal view distinctly constricted on sides; punctuation slightly coarser than on elytra. Scutellum small. Elytra at widest point 1.20-1.25 x wider



19



20



21



22



23

FIGURES 19-23

M. moorei n. sp., Shingle Hill, N. S. W, Australia, male, 0.93 mm: **19**, habitus; **20**, prothorax; **21**, right fore leg; **22**, aedeagus, dorsal, length 294 μ ; **23** idem, lateral.

than prothorax, 1.95-2.18 x longer than own width, dorsally distinctly coriaceous with leather-like surface sculpture at 50x magnification. Femora strongly incrassate, with long, slender peduncle.

Male. Aedeagus 294 μ long by 69 μ wide; internal sac with a flagelliform basal sclerite approximately 1.3 x longer than aedeagus (incl. apodemes).

Length 0.90-0.98 mm.

REMARKS — The locality labels attached to the specimens do not indicate the gum tree species the soil was taken from. The main species at Shingle Hill was *Eucalyptus macrorhyncha* (B. P. Moore, pers. comm.).

Genus **HEXONYMUS** n. gen.

Type species. *H. reginalis* n. sp.

DESCRIPTION — Characters in agreement with those of *Myrtonymus*, differing in having a 6-segmented funicle, a scape at apical third strongly compressed, a prothorax without an apical constriction on sides, extremely fine punctation, very short erect hairs on entire dorsal surface, and an aedeagus with a distinctly pigmented tectum.

DISTRIBUTION — Australia.

ETYMOLOGY — *Hexonymus* is a Greek compound from hex for six, and ónyma for name or designation; gender masculine.

Hexonymus reginalis n. sp.

(Figures 24-27)

TYPE MATERIAL — Holotype male: Australia, 0.85 x 0.25 mm, Queensland, Mt Cook N. P., 15°19'S 145°16'E, 10-12 May 1981, A Calder & J Freehan, in ANIC. Paratypes: same information as holotype, 1 males, 1 female, in ANIC, NZAC.

ETYMOLOGY — The specific name *reginalis* is an adjective of the Latin noun regina, for queen, taken geographically for Queensland.

DESCRIPTION — Reddish-brown. Rostrum plus head slightly shorter than prothorax, 0.91 x length of prothorax, 2.87 x longer than wide across antennal insertions, with fine, yet more coarsely, non-confluent punctation than pronotum; frontal fovea absent. Prothorax 1.08 x longer than wide, gently rounded, in dorsal view with sides continuous through to apex without constriction; punctation, distinct, rather deep, very fine, absent on midline and on middle of apical collar. Scutellum small. Elytra at maximum width 1.27 x wider than prothorax, 2.0 x as long as own width, with obsolescent, very shallow and fine punctation. Femora strongly incrassate, with short, slender peduncle.

Male. Aedeagus 406 μ long; pedon approximately 112 μ long by 59 μ wide, 1.90 x longer than wide, rounded at apex; tectum distinctly pigmented, weakly tapering caudad from basal third, widening towards base and directly joined to apodemes; apodemes more than 2.5 x longer than pedon, weakly pigmented at junction with pedon; internal sac long, exposed to nearly end of apodemes, *in situ* with a pair of contiguous, deeply pigmented frenal sclerites at ostial area, and some irregularly shaped, weakly pigmented blade-like sclerites inside aedeagal body and nearest exposed area of internal sac, and (apparently) with a short flagelliform basal sclerite.

Length 0.75-0.85 mm.

REMARKS — It is likely that a short flagellum is present but is not obvious from the Canada balsam mounted slide.



24



25



26



27

FIGURES 24-27

Hexonymus reginalis n. sp., Mt Cook N. P., Queensland, Australia, male, 0.82 mm: **24**, habitus; **25**, antennae and tip of rostrum; **26**, right fore tibia and tarsus; **27**, aedeagus, length 406 μ .

ACKNOWLEDGMENTS

I wish to express my thanks for collecting the hypogean specimens dealt with in the paper to A. Calder & J. Freehan, R. S. McInnes, B. P. Moore, S. B. & J. Peck, and T. Théry; for the SEM micrographs to I. Hallett and P. Sutherland (Hort Research); for the digital images and drawings to B. Rhode, R. Leschen (Landcare Research), J. Keel, T. Eberhardt and P. Prasad (AsureQuality), J. Kowhai and R. Schnitzler. Special thanks are due to Barry Moore (CSIRO, Canberra) and Thomas Théry (Germaine Cousin Grant, SEF) for collecting the first Myrtonymina of Australia and New Caledonia, to Birgit Rhode (Landcare Research) for adjusting, assembling and numbering the figures on plates, and to Leonie Clunie (Landcare Research) for helpful assistance in management of specimens and loans.

REFERENCES

-
- ALONSO-ZARAZAGA M. A. & LYAL H. C. 1999 — *A world catalogue of families and genera of Curculionoidea (Insecta: Coleoptera)*. Entomopraxis, Barcelona, Spain 315 pp.
- IENISTEA M. A. 1986 — A new hierarchical system of Arthropoda, mainly referring to insects. *Yes Quarterly* 3(2): 13-38.
- KUSCHEL G. 1971 — Entomology of the Aucklands and other islands south of New Zealand: Coleoptera: Curculionidae. *Pacific Insects Monograph* 27: 225-259
- KUSCHEL G. 1990 — Beetles in a suburban environment: a New Zealand case study. The identity and status of Coleoptera in the natural and modified habitats of Lynfield, Auckland (1974-1989). DSIR Plant Protection Report 3: 1-118.
- KUSCHEL G. 1991 — A pitfall trap for hypogean fauna. *Curculio* 31: 5.
- KUSCHEL G. 1995 — A phylogenetic classification of Curculionoidea to families and subfamilies, in ANDERSON R. S. & LYAL C. H. C. (eds) *Biology and phylogeny of Curculionoidea: Proceedings of a symposium convened at the XVIII International Congress of Entomology, Vancouver, Canada, July 3-9, 1988*. *Memoirs of the Entomological Society of Washington* 14: 5-33
- OSELLA G. 1977 — Revisione della sottofamiglia Raymondionyminae (Coleoptera, Curculionidae). *Memorie del Museo Civico di Storia Naturale di Verona*, 2 serie, Sez. Science della Vita 1: 1-162.
- REMILLET M. 1968. — Quelques données écologiques et biologiques sur *Raymondionymus perrisi* Grenier (Coleoptera Curculionidae). *Revue d'Ecologie et de Biologie du Sol* 5(3): 533-547.
- THOMPSON R. T. 1992 — Observations on the morphology and classification of weevils (Coleoptera, Curculionidae) with a key to major groups. *Journal of Natural History* 26: 835-891.
- ZIMMERMAN E. C. 1993 — *Australian Weevils (Coleoptera: Curculionoidea)*, volume 3: *Nanophyidae, Rhynchophoridae, Eirrhiniidae, Curculionidae: Amycterinae, Literature Consulted*. Melbourne: CSIRO, x+854 p.

***Exocelina nehoue* n. sp. from New Caledonia, with a new synonym and new collecting records for other species in the genus (Coleoptera: Dytiscidae)**

Michael Balke⁽¹⁾, Jiří Hájek⁽³⁾, Lars Hendrich⁽¹⁾ & Günther Wewalka⁽⁴⁾

⁽¹⁾ Department of Entomology, Zoological State Collection, Muenchhausenstr. 21, 81247 Munich, Germany
Coleoptera-ZSM@zsm.mwn.de

⁽²⁾ GeoBioCenter, Ludwig-Maximilians-University, Richard-Wagner-Str. 10, 80333 Munich, Germany

⁽³⁾ Department of Entomology, National Museum, Kunratice 1, 148 00 Praha 4, Czech Republic

⁽⁴⁾ Starkfriedgasse 16, Vienna, Austria

ABSTRACT

Exocelina nehoue n. sp. is described based on a single female, collected at light in the North Province of New Caledonia near the Nehoue River. The new species can be distinguished from all other known *Exocelina* species by possession of thirteen strong elytral striae and one submarginal stria on elytron in combination with dominating orange-brown coloration; its status is confirmed with analysis of a fragment of mitochondrial DNA. *Copelatus bilunatus* Guignot, 1955, described on a single male specimen wrongly labelled as collected from Madagascar, is a junior subjective synonym of the New Caledonian *Exocelina subjecta* (Sharp, 1882). New collecting data are presented for the latter and ten other species of New Caledonian *Exocelina*.

RÉSUMÉ

Exocelina nehoue n. sp. de Nouvelle Calédonie, avec une nouvelle synonymie et de nouvelles mentions de collectes d'autres espèces du genre (Coléoptères : Dytiscidae).

Exocelina Nehoue n. sp. est décrit sur la base d'une seule femelle, collectée à la lumière dans la Province Nord de Nouvelle-Calédonie, près de la rivière Nehoue. La nouvelle espèce se distingue de toutes les autres espèces d'*Exocelina* connues par la possession de treize fortes stries sur les élytres et une strie submarginale sur l'élytre en combinaison avec une coloration brun-orangé dominante. Son statut

est confirmé par l'analyse d'un fragment d'ADN mitochondrial. *Copelatus bilunatus* Guignot, 1955, décrit à partir d'un seul spécimen mâle à tort étiqueté comme collecté à Madagascar, est un synonyme junior subjectif de l'espèce néo-calédonienne *Exocelina subjecta* (Sharp, 1882). De nouvelles données de collectes sont présentées pour cette espèce ainsi que pour dix autres espèces d'*Exocelina* de Nouvelle-Calédonie.

INTRODUCTION

New Caledonian water beetles were recently revised or reviewed in a monographic account by Jäch & Balke (2010). With 54 species, the diving beetles (Dytiscidae) are well represented in New Caledonia. Many of them were newly described in Jäch & Balke (2010), most of them in the genus *Exocelina* Broun, 1886, which contained 36 New Caledonian species so far (Wewalka *et al.* 2010). *Exocelina* is otherwise very speciose in New Guinea and Australia.

We here describe a new species of *Exocelina* from the north-western tip of Grande Terre. The new species is only known from the female holotype collected and dry-mounted in 2007. Though morphologically well characterized, we extracted and sequenced a fragment of mitochondrial DNA to characterize our species genetically as well.

In addition, during our recent work on Copelatinae from Madagascar, we have studied the holotype of *Copelatus bilunatus* Guignot, 1955 which was never mentioned since its description. The study revealed that it is in fact a mislabelled New Caledonian *Exocelina* and represents a junior synonym of *E. subjecta* (Sharp, 1882) which we establish below.

Finally, we provide new locality data for *E. aubei* (Montrouzier, 1860), *E. browni* (Guignot, 1942), *E. interrupta* (Perroud & Montrouzier, 1864), *E. lilianae* Wewalka, Balke & Hendrich, 2010, *E. maculata* (Sharp, 1882), *E. nielsi* Wewalka, Balke & Hendrich, 2010, *E. perfecta* (Sharp, 1882), *E. poellabauerae* Wewalka, Balke & Hendrich, 2010, *E. remyi* Wewalka, Balke & Hendrich, 2010 and *E. subjecta*.

MATERIAL AND METHODS

Non destructive DNA extraction was performed with the Qiagen Dneasy tissue kit. DNA laboratory work followed standard procedure for amplification and sequencing of the mitochondrial cytochrome *c* oxidase 1, 3' fragment, detailed on our laboratory wiki: http://zsm-entomology.de/wiki/The_Beetle_D_N_A_Lab. Data information content was visualized as a neighbour joining diagram generated in the computer program PAUP*. The sequence data was submitted to GenBank and has accession number FR774193.

The habitus photography was derived from an image stack, assembled with the program HELICON FOCUS, produced with a NIKON D700 camera equipped with a bellows and a LEICA PHOTAR 25 mm. A high resolution file of the habitus image has been stored at: www.species-id.net/o/index.php?title=File:Exocelina_nehoue_DorsHab.tiff&oldid=110327.

Exact label data are cited for the material. A forward slash (/) separates different lines of data. Additional remarks are found in square brackets.

The specimens included in this study are deposited in the following institutional and private collections:

CFP Collection Fernando Pederzani, Ravenna, Italy.

CLH Collection Lars Hendrich, Munich, Germany.

MNHN Muséum national d'Histoire naturelle, Paris, France.

NMPC Národní muzeum, Praha, Czech Republic.

NZAC New Zealand Arthropod collection, Auckland, New Zealand.

ZSM Zoologische Staatssammlung München, Germany.

SYSTEMATIC PART

Family DYTISCIDAE Leach, 1815

Genus *EXOCELINA* Broun, 1886

Exocelina nehoue n. sp.

Figures 1-3

See also: www.species-id.net/o/index.php?title=File:Exocelina_nehoue_DorsHab.tiff&oldid=110327

TYPE MATERIAL — Holotype female: “New Caledonia (N) / 20°25.2 S 164°13.3E / Nehoue river, 15 m / 8.01.2007 public camp site / night coll. (lamp & beating) / leg. M. Wanat & R. Dobosz”, “Muzeum Przyrodnicze Uniwersytetu Wrocławskiego / MNHW / Museum of Natural History / Wrocław University “Exocelina / spec. nov. / det. Wewalka 2009 / (female symbol)” (MNHN). We attached our red holotype label.

TYPE LOCALITY — New Caledonia, Grande Terre, North Province, Nehoue River.

DESCRIPTION — *Habitus* (Figure 1). Body regularly oblong-oval, broadest in middle; moderately convex; pronotum broadest between posterior angles, lateral margins distinctly curved; base of elytra as broad as pronotal base; lateral margins of elytra moderately and regularly curved.

Measurements of holotype. Length of body 5.8 mm; Length of body minus head 5.5 mm; greatest width of body 3.0 mm.

Color. Head blackish, clypeus and frons dark-brown to reddish-brown. Pronotum blackish in middle, dark-brown to reddish-brown towards lateral margins, distinctly lighter, orange-brown along lateral margins. Elytra dark-brown to orange-brown. Epipleura dark-brown, rest of ventral surface black to dark-brown. Antennae and legs reddish or orange-brown.

Surface sculpture. Head with distinct microreticulation of small regular polygonal cells, with fine, regular, comparably sparse punctation (size of punctures equals that of cells) and with some strong, short, irregular longitudinal striae on frons. Pronotum with microreticulation and fine punctation as on head; with comparably dense and strong, short or moderately long, irregular longitudinal striae, missing only discally and along all sides. Elytron with very fine microreticulation and with fine, sparse punctation as on head and pronotum; with thirteen strong longitudinal striae and one submarginal stria; striae 4, 10, 12, 13 shorter apically, latter two only slightly so; stria 3 short anteriorly, only visible on posterior 1/2 or 2/5 of elytron.



FIGURE 1

Exocelina nehoue n. sp., holotype,
dorsal habitus and coloration.

Structures. Pronotum with fine lateral rim, missing only on anterior corners; with moderate impressions along lateral margins; posterior corners of pronotum rectangular, slightly truncate. Prosternal process convex (or raised medially) but not keeled.

Male unknown.

AFFINITIES — *Exocelina nehoue* n. sp. can be distinguished from all other known *Exocelina* species by possession of thirteen strong striae (the third one being short anteriorly) and one submarginal stria on elytron in combination with dominating orange-brown dorsal coloration. The widespread New Caledonian *E. aubei* appears similar, but the dorsal coloration is much darker, dark-brown to blackish, and *E. aubei* only possesses 12 striae plus a submarginal stria on elytron (see Wewalka *et al.* 2010). The *cox1* sequence data we obtained confirm that *Exocelina nehoue* n. sp. and *E. aubei* are indeed very distinctive (Figure 2).

HABITAT — Unknown, collected at light.

DISTRIBUTION — Only known from the type locality (Figure 3).

Exocelina subjecta (Sharp, 1882)

Copelatus subjectus Sharp, 1882: 568 (original description, New Caledonia).

Copelatus bilunatus Guignot: 1955: 73 (original description, Madagascar [mislabelled]) syn. nov.

Exocelina subjecta – Wewalka *et al.* 2010: 68 (new combination, redescription).

TYPE MATERIAL — *Copelatus bilunatus*. Holotype male: “Madagascar [printed] // nov. sp. [handwritten]”, “Type [red label with black margin, printed]”, “F. Guignot det. 1942 [printed, “4” crossed by handwriting] 54 [handwritten] / Copelatus / bilunatus Guign. / Type (male symbol). [Guignot’s handwriting]” (ZSM).

ADDITIONAL MATERIAL EXAMINED — In addition to material mentioned in Wewalka *et al.* (2010), we have seen following specimens: 2 exs. “New Caledonia, Col d’Amieu, 450 m, 16 Oct 1978, G. Kuschel” (NZAC); 4 exs. “New Caledonia, Col d’Amieu, Forestry Camp, 14-15 Nov 1988, J.S. Dugdale &”, “B. Frerot, to light” (NZAC); 2 exs. “New Caledonia Prov. Sud, Mt. Mou cca 10 km NW Paita 07.-12.01.2005 A. Kudrna Jr. lgt.” (CFP); 4 exs. “New Caledonia Prov. Sud, Parc Prov. Rivière Bleue 02.-09.12.2004 A. Kudrna Jr. lgt.” (CFP); 1 ex. “New Caledonia Province Sud, environs of Boulouparis 09.-16.02.2009 A. Kudrna Jr. lgt.” (CFP).

NOTES ON CLASSIFICATION — Based on presence of metacoxal lines, Guignot (1955) classified the species in the genus *Copelatus* Erichson, 1832. Because of non striate elytra, the species was later placed in the *Copelatus hydroporoides* (or *haemorrhoidalis*, in earlier studies) species group, see, *e.g.* Nilsson (2001).

The single male specimen indeed possesses complete metacoxal lines and only weakly dilated pro- and mesotarsomeres I–III with eight adhesive discs, which enables its classification in *Copelatus*. However it has also a stout, spin-like seta on anterodistal angle of protarsomere IV, which refers to its placement in predominantly Austro-pacific genus *Exocelina* and suggest, that the specimens was mislabelled. When we compared the type of *C. bilunatus* with extensive material of *Exocelina* from New Caledonia (see Wewalka *et al.* 2010), we have found, that it is identical in all details with common New Caledonian species *Exocelina subjecta* (Sharp, 1882). Therefore, we consider *C. bilunatus* to be a junior subjective synonym of the later species.

DISTRIBUTION — New Caledonia: North & South Province (Wewalka *et al.* 2010).

FIGURE 2

Neighbour joining diagram for 3' *cox1* sequences of New Caledonian *Exocelina* species, indicating distinctiveness of *Exocelina nehoue* n. sp. relative to the morphologically similar *E. aubei* and all other species for which data were available.

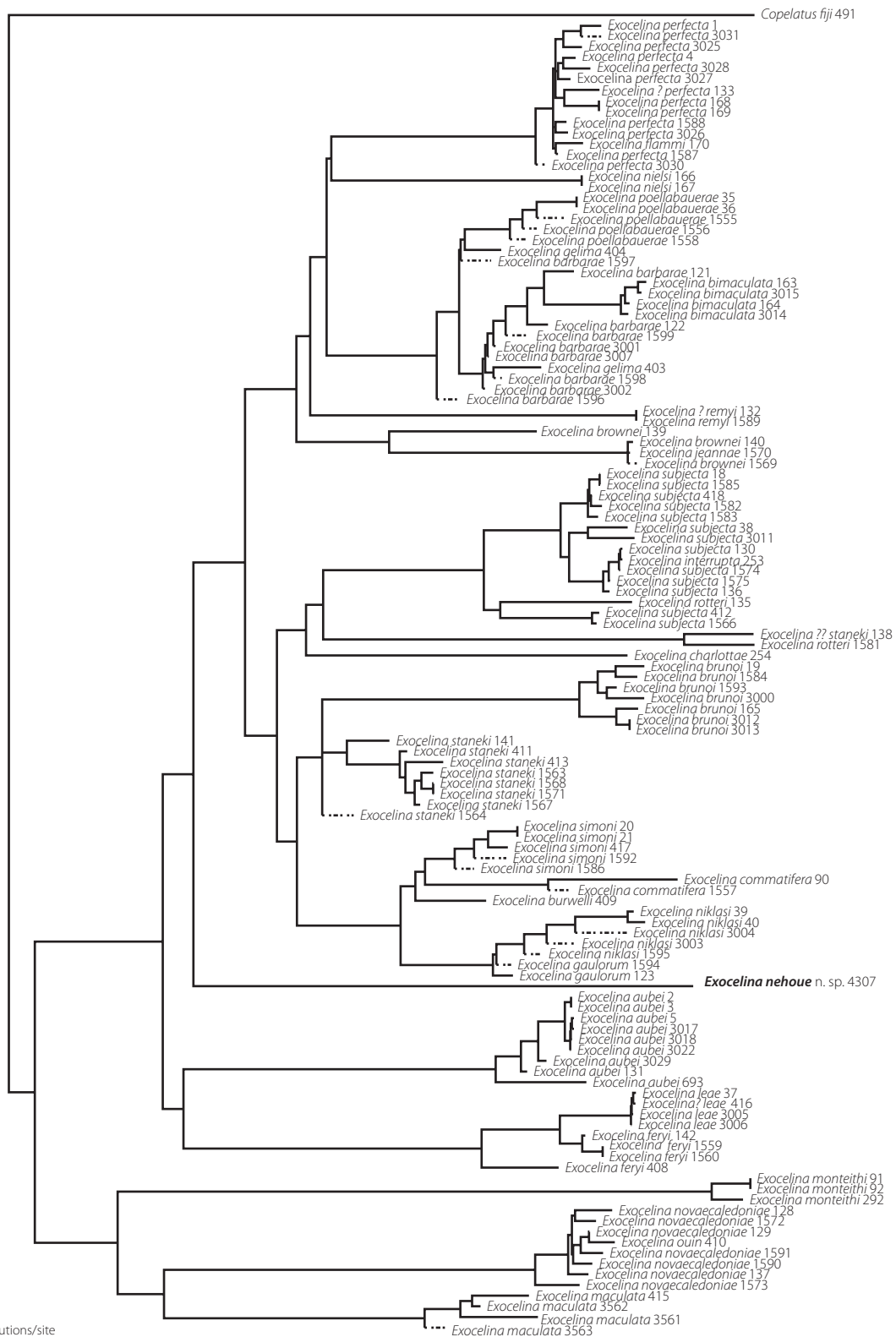




FIGURE 3
Exocelina nehoue n. sp.,
 distribution on Grande Terre,
 New Caledonia.

NEW RECORDS

Exocelina aubei (Montrouzier, 1860)

Copelatus aubei Montrouzier, 1860: 244

Exocelina aubei – Nilsson 2007: 33

MATERIAL EXAMINED — 2 exs. “New Caledonia Prov. Sud, Parc Prov. Rivière Bleue 02.-09.12.2004 A. Kudrna Jr. lgt.” (CFP); 2 exs. “New Caledonia Prov. Sud, Parc Prov. Rivière Bleue near gate 13.-14.02.2005 A. Kudrna Jr. lgt.” (CFP); 3 exs. “New Caledonia Prov. Sud, Near Bouraké 10 km SW Bouloupairi 03.-07.01.2005 A. Kudrna Jr. lgt.” (CFP); 8 exs. “New Caledonia Prov. Sud, Mt. Mou cca 10 km NW Paita 07.-12.01.2005 A. Kudrna Jr. lgt.” (CFP); 1 ex. “New Caledonia Prov. Sud, around Sarraméa 22.-23.12.2004 A. Kudrna Jr. lgt.” (CFP); 1 ex., “New Caledonia Prov. Sud, environs of Sarraméa 05.-08.02 and 16.-18.02.2009 A. Kudrna Jr. lgt.” (CFP); 1 ex. “New Caledonia Prov. Sud, village Bouirou cca 20 km N Bourail 09.-10.12.2008 500m. A. Kudrna Jr. lgt.” (CFP).

DISTRIBUTION — New Caledonia: North & South Province, Île Art, Île des Pins (Wewalka *et al.* 2010).

Exocelina bimaculata (Perroud & Montrouzier, 1869)

Colymbetes bimaculata Perroud & Montrouzier, 1869: 78

Exocelina bimaculata – Nilsson 2007: 33

MATERIAL EXAMINED — 1 ex. "New Caledonia, P.D.Montague, 1918-87", "Loc. Paombai [Pombeï], Date 16.9.[19]14, Coll. P.D.Montague, New Caledonia Exped." (NZAC).

DISTRIBUTION — New Caledonia: North Province (Wewalka *et al.* 2010).

Exocelina brownei (Guignot, 1942)

Copelatus brownei Guignot, 1942: 86

Exocelina brownei – Nilsson 2007: 33

MATERIAL EXAMINED — 1 ex. "New Caledonia, Mt Dore, in forest at coast, 8 Oct 1978, J.S.Dugdale" (NZAC); 8 exs., "New Caledonia Province Sud, environs of Boulouparis 09.-16.02.2009 A. Kudrna Jr. Igt." (CFP, CLH).

DISTRIBUTION — New Caledonia: North & South Province (Wewalka *et al.* 2010).

Exocelina interrupta (Perroud & Montrouzier, 1864)

Agabus interrupta Perroud & Montrouzier, 1864: 79

Exocelina interrupta – Nilsson 2007: 33

MATERIAL EXAMINED — 1 ex. "New Caledonia Prov. Sud, Mt. Mou ca 10 km NW Paita 07.-12.01.2005 A. Kudrna Jr. Igt." (CFP).

DISTRIBUTION — New Caledonia: South Province (Wewalka *et al.* 2010).

Exocelina lilianae Wewalka, Balke & Hendrich, 2010

Exocelina lilianae Wewalka, Balke & Hendrich, 2010: 70

MATERIAL EXAMINED — 1 ex. "New Caledonia, Rivière Bleue, 11 Nov 1988, J.S. Dugdale & B. Frerot" (NZAC); 2 exs. "New Caledonia Prov. Sud, Parc Prov. Rivière Bleue inside park 14.-16.02.2005 A. Kudrna Jr. Igt." (CFP).

DISTRIBUTION — New Caledonia: South Province (Wewalka *et al.* 2010).

Exocelina maculata (Sharp, 1882)

Copelatus maculata Sharp, 1882: 566

Exocelina maculata – Nilsson 2007: 33

MATERIAL EXAMINED — 6 exs. "New Caledonia, Mt. Humbolt, 1300 m, 12 Nov 1982, W.J. Winstanley" "in pools in intermittent stream" (NZAC, NMPC).

DISTRIBUTION — New Caledonia: South Province (Wewalka *et al.* 2010).

Exocelina nielsi Wewalka, Balke & Hendrich, 2010

Exocelina nielsi Wewalka, Balke & Hendrich, 2010: 91

MATERIAL EXAMINED — 1 ex. "New Caledonia Province Sud, environs of Boulouparis 09.-16.02.2009 A. Kudrna Jr. lgt." (CFP).

DISTRIBUTION — New Caledonia: North & South Province (Wewalka *et al.* 2010).

Exocelina perfecta (Sharp, 1882)

Copelatus perfecta Sharp, 1882: 593

Exocelina perfecta – Nilsson 2007: 33

MATERIAL EXAMINED — 6 exs. "New Caledonia Prov. Sud, Mt. Mou cca 10 km NW Paita 07.-12.01.2005 A. Kudrna Jr. lgt." (CFP, CLH).

DISTRIBUTION — New Caledonia: North & South Province (Wewalka *et al.* 2010).

Exocelina poellabauerae Wewalka, Balke & Hendrich, 2010

Exocelina poellabauerae Wewalka, Balke & Hendrich, 2010: 82

MATERIAL EXAMINED — 4 exs. "Nouvelle Calédonie, Grande Terre 30.3.-12.4.1994 L. & R. Businsky lgt." (CFP, CLH).

DISTRIBUTION — New Caledonia: North Province, Mount Panié (Wewalka *et al.* 2010).

Exocelina remyi Wewalka, Balke & Hendrich, 2010

Exocelina remyi Wewalka, Balke & Hendrich, 2010: 90

MATERIAL EXAMINED — 5 exs. "New Caledonia Prov. Sud, Mt. Mou cca 10 km NW Paita 07.-12.01.2005 A. Kudrna Jr. lgt." (CFP, CLH).

DISTRIBUTION — New Caledonia: South Province (Wewalka *et al.* 2010).

ACKNOWLEDGMENTS

We thank M. Wanat (Wrocław, Poland), F. Pederzani (Ravenna, Italy) and R.A.B. Leschen (NZAC) for the opportunity to study these beetles, and Arnaud Faille for help in the DNA laboratory. This project was funded by German Science Foundation DFG grant BA2152/7-1.

REFERENCES

- GUIGNOT F. 1955 — Dytiscides inédits de la collection Zimmermann (Col. Dytiscidae). *Annales de la Société Entomologique de France* 123(1954): 67–73.
- JÄCH M.A. & BALKE M. (eds) 2010 — *Water beetles of New Caledonia* (part 1). *Monographs on Coleoptera* 3 : IV+449 pp.
- NILSSON A.N. 2001 — *Dytiscidae (Coleoptera)*. World Catalogue of Insects 3: 1–395.
- WEWALKA G., BALKE M. & HENDRICH L. 2010 — Dytiscidae: Copelatinae (Coleoptera), in JÄCH, M.A. & BALKE, M. (eds), *Water beetles of New Caledonia* (part 1), *Monographs on Coleoptera* 3: 45–128.

A new species, new records, and notes on biology of New Caledonian *Scirtes* Illiger (Insecta: Coleoptera: Scirtidae)

Rafał Ruta

University of Wrocław, Department of Biodiversity and Evolutionary Taxonomy – Przybyszewskiego 63/77 – 51-148 Wrocław – Poland
scirtes@biol.uni.wroc.pl

ABSTRACT

Scirtes gelimensis n. sp. is described from the vicinity of Canala, New Caledonia. Notes on the morphology of females of New Caledonian *Scirtes* are provided. New localities of three species are reported. Notes on biology and habitats of New Caledonian *Scirtes* are given.

RÉSUMÉ

Une nouvelle espèce, des nouvelles signalisations et des notes sur la biologie de *Scirtes* Illiger (Insectes : Coléoptères : Scirtidae).

Scirtes gelimensis n. sp. est décrite des environs de Canala, Nouvelle-Calédonie. Des notes sur la morphologie des femelles de *Scirtes* calédoniens sont fournies. Des nouvelles localités de trois espèces sont signalées. Des notes sur la biologie et l'habitat des *Scirtes* de Nouvelle-Calédonie sont données.

INTRODUCTION

New Caledonian *Scirtes* Illiger have been recently revised by Ruta & Yoshitomi (2010a). During two recent expeditions, new data have accumulated, and an undescribed species was collected. In the present paper a new species is described, notes on the morphology of females of New Caledonian *Scirtes* are provided, new records of previously known species are reported and biological observations are summarized.

MATERIALS AND METHODS

Specimens were collected in ethanol or killed with ethyl acetate. Abdomens were removed and transferred into 10% aquatic NaOH solution. After *ca* 6 hours genitalia were removed, washed in distilled water, stained in chlorazol black solution, and then observed in glycerin or Swann's medium (gum - chloral hydrate medium). Observations were made under Nikon Eclipse E600 compound microscope and Nikon SMZ 1500 dissecting microscope, both with a Nikon Coolpix 4500 camera attached. Images were generated using Helicon Focus 4.62 software and enhanced using Photoshop CS3. Selected specimens were studied with the use of a scanning electron microscope (HITACHI S-3400N) in the laboratory of the Museum and Institute of Zoology, PAS in Warsaw.

Depositories.

DBET: Department of Biodiversity and Evolutionary Taxonomy, University of Wrocław, Poland

MNHN: Muséum national d'Histoire naturelle, Paris, France

USMB: Upper Silesian Museum, Bytom, Poland

The following abbreviations are employed:

EL – maximum elytral length, EW – maximum elytral width, HL – maximum head length, HW – maximum head width, PL – maximum pronotal length, PW – maximum pronotal width, TL – total length (measured from anterior margin of the pronotum to the elytral apex).

TAXONOMIC PART

Family SCIRTIDAE Fleming, 1821

Genus *SCIRTES* Illiger, 1807

Scirtes gelimensis n. sp.

Figures 1, 3-8

TYPE MATERIAL — Holotype, male: New Caledonia (N) \ -21.5779/165.9719 \ Canala, 4 km S of Mia \ 30.11.2010, 380 m, rd end \ Gélina river valley, at light \ leg. R. Ruta, M. Wanat. Temporarily deposited in DBET, final depository: MNHN.

TYPE LOCALITY — Canala vic., Gélina riv. valley.

DIAGNOSIS — The species externally resembles *Scirtes vittatus* Ruta & Yoshitomi 2010 in having blackish elytra with a yellow suture. It can be distinguished from related species only on the basis of the morphology of male genitalia: Y-shaped tegmen and asymmetrical penis with three long and narrow processes which are regularly narrowing till apices.

DESCRIPTION — Holotype, male (Figure 1). Measurements (mm): TL 2.70, EW 1.90, EL 2.35, PW 1.25, PL 0.5, HW 0.75, HL 0.5, interocular space 0.45. Body broadly oval, slightly depressed, covered with suberect brown setae. Head and pronotum yellowish, base of pronotum dark brown, transverse stripe in basal 1/3 of pronotum yellowish-brown, posterior portion of elytra brownish, suture yellow, antennae yellowish, slightly darkened apically, legs yellowish-brown, ventrum brownish. Body 1.4 times as long as broad. Head 1.7 times wider than interocular space, with distinct punctation, punctures separated by *ca* 0.5-1.0 diameter, eyes finely faceted, strongly protuberant. Antennae filiform, antennomeres 1 and 2 subcylindrical, antennomere 3 as long as 2 and slightly narrower than remaining ones, antennomeres 4 *ca*



FIGURES 1-2

1, *Scirtes gelimensis* n. sp., holotype, habitus. 2, *Scirtes* sp., female, habitus. Scale bar = 1.0 mm.

1.5 times longer than 3, antennomeres 5–11 of subequal length, slightly shorter than antennomere 4. Anterior clypeal margin straight, sides of clypeus subparallel, anterolateral angles slightly rounded. Labrum small, partly hidden under clypeus. Mandibles short, subtriangular, without denticles on mesal edges. Pronotum transverse, 2.5 times wider than long, widest at posterior angles; disc with distinct punctation (punctures separated by 1.0 diameter); posterior margin subtly bisinuate; anterior angles slightly explanate; posterior angles right angled; sides subtly rounded. Scutellum subtriangular, punctation more or less as on pronotum. Angle between pronotum and elytra not marked in dorsal outline. Elytra with subtle traces of two longitudinal ridges, and slightly marked adsutural stria, 1.2 times as long as broad and 4.7 times as long as pronotum, broadest slightly before middle of its length. Sides rounded, converging to apex in posterior half. Humeri well marked. Punctuation strong, distance between punctures *ca* 1.0 diameter. Hind wings fully developed. Prosternal process relatively narrow, almost laminate. Mesocoxae separated by a subparallel-sided process, about 3 x longer than its greatest width, slightly diverging apically. Abdominal ventrite 5 slightly emarginated apically. Left metatibia broken, and right hind leg missing in the holotype. Male genitalia (Figures 3-8). Penis (L 0.91, W 0.31) asymmetrical with three long and narrow processes; median process longest, gradually narrowing in apical half; shortest process very thin, *ca* 2 times shorter than longest process; third process as long as two thirds length of longest process, of subequal width, triangularly tempered at apex; tegmen (L 0.82, W 0.17) elongate Y-shaped, parameres *ca* 1.5 times as long as basal (undivided) part; tergite 8 (L 0.50, W 0.39) with a row of short setae at apex; tergite 9 (L 0.48, W 0.22) consists of two hemitergites, apical margin sparsely covered with setae; sternite 8 (W 0.21) very small, in a form of a transverse plate; sternite 9 (L 0.29, W 0.27) small, consisting of two subtriangular hemisternites, apical setation sparse.

Female unknown.

ETYMOLOGY — After Gélima river, in which valley the holotype was collected.



FIGURES 3-8

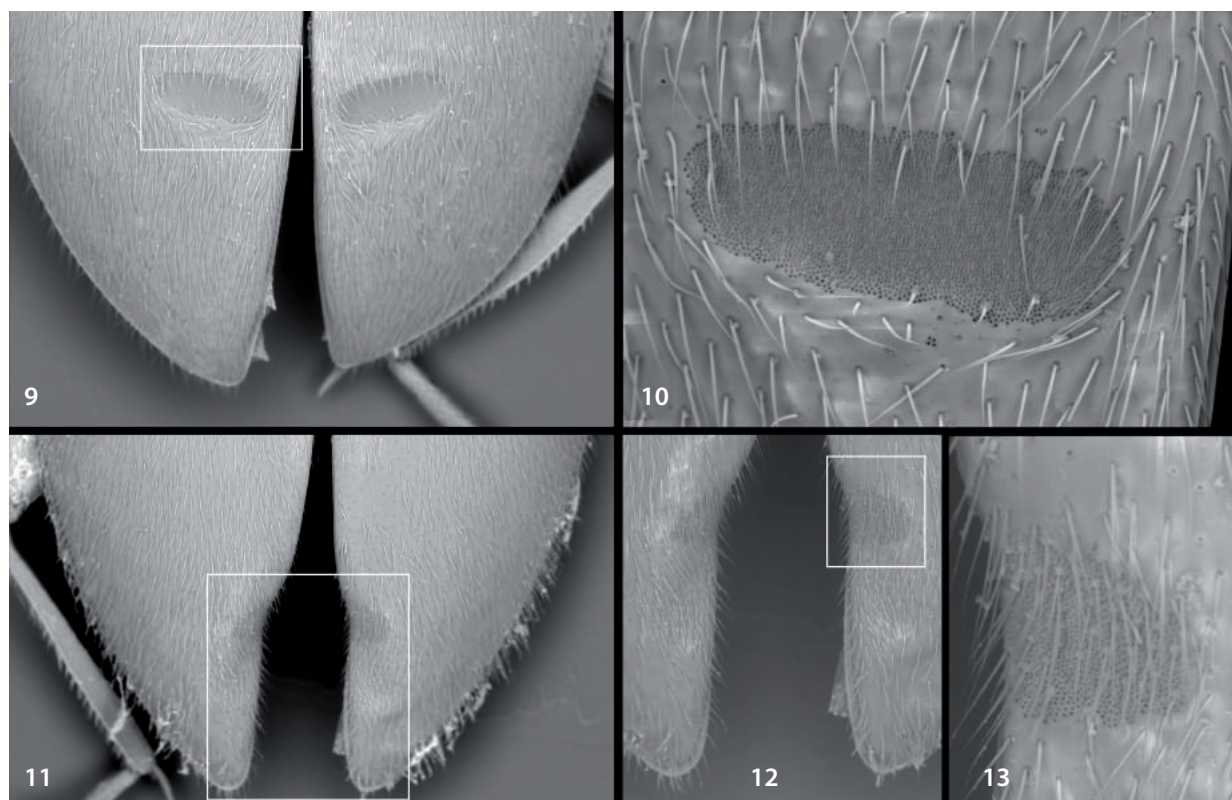
Scirtes gelimensis n. sp., male genitalia. **3.** Penis. **4.** Apical portion of penis, close-up. **5.** Tegmen. **6.** Tergite **8.** **7.** Tergite **9.** **8.** Sternites **8** & **9.** Scale bar = 0.5 mm.

MORPHOLOGICAL NOTES ON FEMALES OF NEW CALEDONIAN SCIRTES

Well developed excitators (sensu Ruta 2008), which are probably secretory structures, were noticed in females of *Scirtes caledonicus* (Ruta & Yoshitomi 2010a). No detailed account on their morphology has been presented till now. They have form of transversely oval depressions in the posterior half of elytra. Examination with a use of a SEM revealed that surface of depressions is densely covered with pores (Figures 9-10).

Female specimen of an undescribed species (Figure 2, TL 2.96) with well developed excitators was recently collected in South Province of New Caledonia (South Province, -21.0137/166.4640, Mt Ouin Rd, 1.9 km N of Dzumac jct, 900m, small stream overgrown with *Blechnum* sp., 4.12.2010, 1 ex., leg. R. Ruta (DBET), Figure 20). Its excitator is illustrated on Figures 11-13. It is cordiform, situated in adsutural region of posterior portion of elytra, and covered with pores.

Very little is known on the variation of female genitalia in Scirtidae. Until now it was reported for *Exochomoscirtes discoidalis* (Pic), which may be a complex of cryptic species (Ruta & Yoshitomi 2010b). To analyse variation of female genitalia of *Scirtes caledonicus*, available specimens were dissected. Remarkable differences in the morphology of bursal sclerite and prehensor were noticed. Bursal sclerite is ring shaped, but may have a well developed denticle on inner margin, and prehensor can be more or less elongated. Morphological differences are summarised in Table 1 and illustrated on Figures 14-17. It is suspected, that the differences result from infraspecific variation.



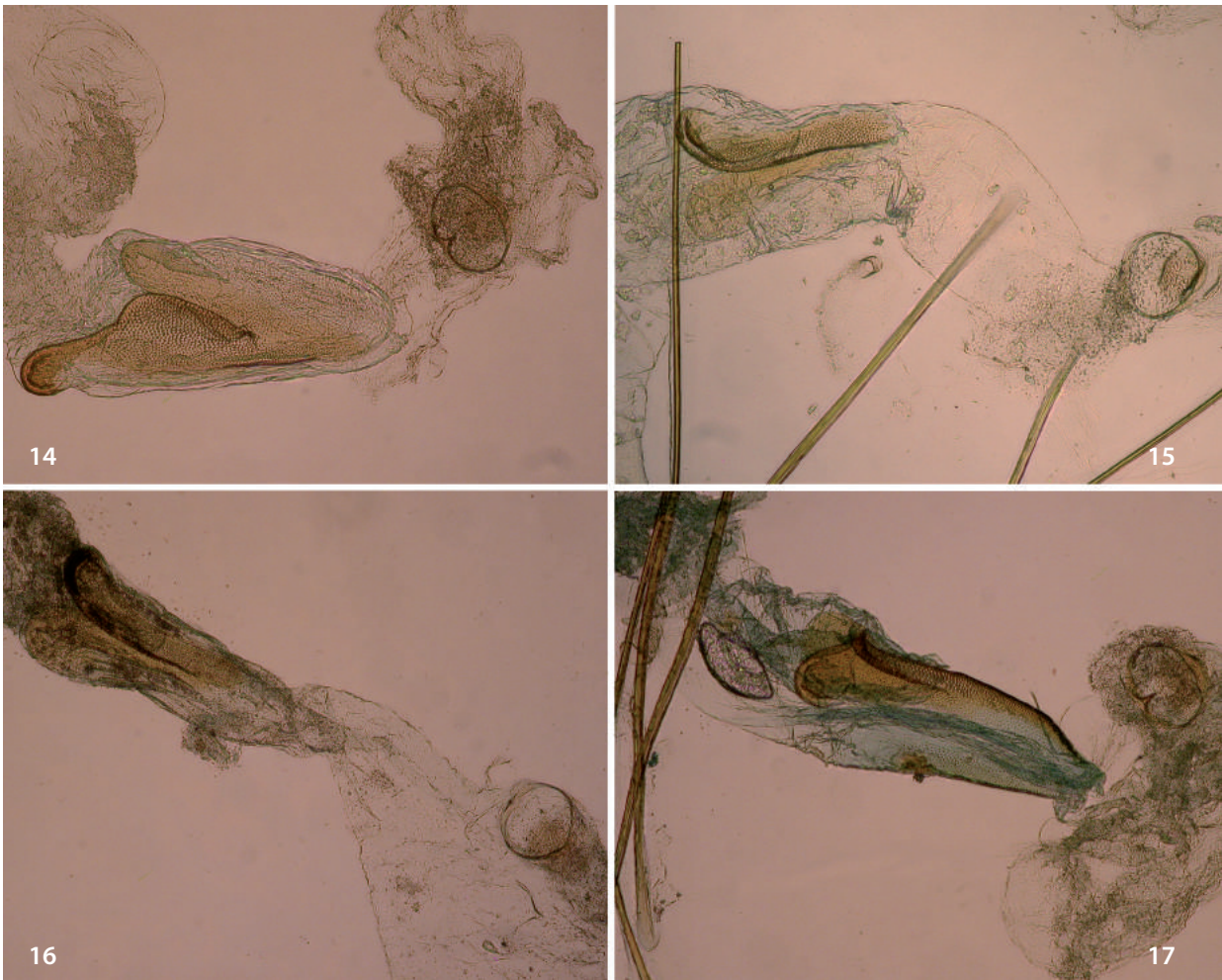
FIGURES 9-13

9-10, *Scirtes caledonicus*. 11-13, *Scirtes* sp. 9, 11, apical portion of elytra. 10, 12, 13, details of excitators.

TABLE 1

Variability of female genitalia of *Scirtes caledonicus* Bourgeois. Label data of the specimens: "Bois" – Bois du Sud, 20.10.2008, leg. M. Wanat (Ruta & Yoshitomi 2010a); "Dumbea" – R. Dumbéa, 4.09.1955 (Ruta & Yoshitomi 2010a); "Thy" – Parc Nat. Thy, 21.3.1999, leg. S. Bily, (Ruta & Yoshitomi 2010a); "Canala" - Canala, 4 km S of Mia, 30.11.2010, leg. R. Ruta (see "New records" below).

Specimen	Bursal sclerite	Prehensor	Figure
"Bois"	ring-shaped, with well marked denticle (0.13)	asymmetrical, L 0.70	14
"Dumbea"	ring-shaped, with subtly marked denticle (0.14)	symmetrical, L 0.41	15
"Thy"	ring-shaped, with subtly marked denticle (0.13)	symmetrical, L 0.55	16
"Canala"	ring-shaped, with well marked denticle (0.13)	symmetrical, L 0.59	17



FIGURES 14-17

Prehensor and bursal sclerite of *Scirtes caledonicus* Bourgeois: **14**, specimen "Bois". **15**, specimen "Dumbea". **16**, specimen "Thy". **17**, specimen "Canala".

**FIGURES 18-23**

Habitats of New Caledonian *Scirtes*: **18-19**, Gélima river valley, type locality of *Scirtes gelimensis* n. sp. **20**, Mt. Dzumac area, collecting site of a female of *Scirtes* sp. **21**, La Capture, stream with larvae of *Scirtes wanati*. **22**, Bois du Sud, locality of *Scirtes caledonicus*, and *Scirtes ebenus*. **23**, Pandanaceae with phytotelmata and larvae of *Scirtes* sp.

NEW RECORDS

Scirtes caledonicus Bourgeois, 1884*Scirtes caledonicus* Bourgeois, 1884: 284

North Province, -21.5779/165.9719, Canala, 4 km S of Mia, 380 m, road end, Gélina river valley, rainforest, 30.11.2010, 1 female beaten from trees by the river, leg. M. Wanat, 30.11/1.12.2010, 1 female under stone near river, leg. R. Ruta (DBET).

South Province, -22.1759/166.7625, Bois du Sud, 220 m, 9.12.2010, 1 female beaten from riverside bushes, leg. R. Ruta (DBET).

Known from several scattered localities on the Grande Terre.

Scirtes ebenus Ruta & Yoshitomi, 2010*Scirtes ebenus* Ruta & Yoshitomi, 2010: 416

South Province, -22.1740/166.7627, Bois du Sud, 220 m, 8.12.2010, 1 male at light, leg. M. Wanat (DBET).

A rare species, recorded only from the Rivière Bleue Provincial Park.

Scirtes wanati Ruta & Yoshitomi, 2010*Scirtes wanati* Ruta & Yoshitomi, 2010: 432

South Province, -22.2267/166.8516, Netcha, Riv. des Lacs, 250 m, 31.10.2010, maquis, 8 males on flowering *Grevillea* sp., leg. R. Ruta (DBET).

South Province, -22.2660/166.8243, La Capture, 260 m, small stream, 1.11.2010 maquis, 4 adults and numerous larvae and pupae under stones, leg. R. Ruta, M. Wanat (DBET).

South Province, -22.1626/166.9243, Yaté env., Niüwede Riv., 8 m, at light, 2.03.2008, 1 male & 1 female, leg. R. Dobosz & T. Blaik (USMB).

Common species restricted to the Southern part of Grande Terre.

NOTES ON THE BIOLOGY OF NEW CALEDONIAN *SCIRTES*

Populations of New Caledonian *Scirtes* spp. usually have very low densities. The only exception is *Scirtes wanati*, which is a very common species in the southern part of the island, especially in the Plaine des Lacs area. Habitats of New Caledonian *Scirtes* are illustrated on Figures 18-23.

Development. New Caledonian *Scirtes* usually develop in slowly running streams. Numerous larvae of *Scirtes wanati* were observed in a small, slowly running and shallow stream in the Plaine des Lacs region. It was noticed that pupation of *Scirtes wanati* takes place under submerged stones. Larvae of some species dwell in phytotelmata developing in Pandanaceae. Numerous larvae of *Scirtes* inhabiting such microhabitats were found in November in Aoupinié and Mt. Panié. They were not associated with adults, but it is plausible, that they belong to *Scirtes nehouensis* (larvae have relatively large body, *Scirtes nehouensis* is known from the Northern part of the island and has been usually collected between January and April).

Adult behavior. Females are easier to collect by beating vegetation close to rivers and streams, or even under rocks on banks of water bodies. Males on the other hand are more often attracted to light. It is plausible that females spend more time closer to the sites of larval development, whereas males are penetrating larger areas in search for females.

Feeding habits. *Scirtes wanati* was observed to feed on flowering *Grevillea* sp. (Proteaceae). Feeding habits of the other species are unknown.

ACKNOWLEDGMENTS

Direction de l'Environnement (Province Sud) and Direction du Développement Economique et de l'Environnement (Province Nord) are thanked for the issuance of collecting permits. Marek Wanat is greatly thanked for inviting me to join his expedition, and both him and Katarzyna Żuk are thanked for their company during our stay at New Caledonia. Jörn Theuerkauf and Paweł Krzyżyński are thanked for invaluable help during the expedition. I would like to thank also Roland Dobosz (USMB) for providing materials for examination.

REFERENCES

-
- BOURGEOIS J. 1884 — Dascillides & Malacodermes de Nouvelle-Calédonie. *Revue d'entomologie* 3: 278-290.
- RUTA R. 2008 — Contribution to the knowledge of Seychellois Scirtidae (Coleoptera: Scirtoidea). *Zootaxa* 1913: 49-68.
- RUTA R. & YOSHITOMI H. 2010a — SCIRTIDAE: The genus *Scirtes* ILLIGER (Coleoptera), in JÄCH & BALKE (eds), Monographs on Coleoptera, Water beetles of New Caledonia (part 1). *Zoologisch-Botanische Gesellschaft and Wiener Coleopterologenverein*, Vienna: 403-438.
- RUTA R. & YOSHITOMI H. 2010b — Revision of the genus *Exochomoscirtes* Pic (Coleoptera: Scirtidae: Scirtinae). *Zootaxa* 2598: 1-80.

***Corindia* (Diptera: Dolichopodidae) from New Caledonia and the Papuan Region**

Daniel J. Bickel

Australian Museum, 6 College Street, Sydney, NSW 2010 Australia
danb@austmus.gov.au

ABSTRACT

The genus *Corindia* Bickel (Diptera: Dolichopodidae: Medeterinae) is described from Melanesia, with two new species from New Caledonia, *C. amieuensis* and *C. flaviscuta*, and one new species from New Ireland, Papua New Guinea, *C. mulleri*. These three species are similar to the described Australian species, and are probably biogeographically linked through the Melanesian archipelago.

RÉSUMÉ

***Corindia* (Diptères : Dolichopodidae) de Nouvelle-Calédonie et de la région Papoue.**

Le genre *Corindia* Bickel (Diptera : Dolichopodidae : Medeterinae) est décrit de la Mélanésie, avec deux nouvelles espèces de Nouvelle-Calédonie, *C. amieuensis* et *C. flaviscuta* et une nouvelle espèce de Nouvelle-Irlande, Papouasie-Nouvelle-Guinée, *C. mulleri*. Ces trois espèces sont similaires aux espèces australiennes décrites et sont probablement biogéographiquement liées à travers l'archipel mélanésien.

INTRODUCTION

Corindia was originally described based on nine species from Australia (Bickel 1986) and three additional species were subsequently described from the Afrotropical region (Grichanov 1998). The genus is also known from undescribed species in the Neotropical region (Bickel 2009).

Corindia is a weakly defined genus and was once considered to be the sister group of *Thrypticus* Gerstacker, a genus defined by the strong synapomorphy of a sclerotised plant-piercing oviscapt (Bickel 1986). However, a more realistic assessment suggests *Corindia* represents a plesiomorphic and paraphyletic assemblage from which *Thrypticus* arose (Bickel & Hernandez 2004). Such paraphyletic genera are a reality among many insect families (much to the horror of cladistic purists), but nevertheless have an important role as name bearers for many species, both described and those awaiting description. And even within paraphyletic genera, monophyletic species groups can be delimited to aid in future phylogenetic analysis.

This paper described three new species of Melanesian *Corindia*, from New Caledonia and New Guinea, all of which show a close relationship to the Australian fauna.

MATERIALS AND METHODS

This study is based on institutional holdings of Melanesian *Corindia* (for institutional repositories and their acronyms, see Acknowledgments, below).

Species are defined primarily on the basis of male characters, especially the genitalia. Drawings of genitalia were made with a camera lucida. The left lateral view of the hypopygium or male genital capsule is illustrated for all three species. In describing the hypopygium, ‘dorsal’ and ‘ventral’ refer to morphological position prior to genitalic rotation and flexion. Thus, in figures showing a lateral view of the hypopygium, the top of the page is morphologically ventral, while the bottom is dorsal. Body length of males is measured from the base of the antennae to the tip of the seventh abdominal segment. The CuAx ratio is the length of the m-cu crossvein/distal section CuA1. The position of features on elongate structures such as leg segments is given as a fraction of the total length, starting from the base. The relative lengths of the podomeres are representative ratios and not measurements, and are given for each leg in the following formula and punctuation: trochanter + femur; tibia; tarsomere 1/ 2/ 3/ 4/ 5. The following abbreviations and terms are used: MSSC - Male secondary sexual character(s), non-genitalic characters found only on male body; I, II, III: pro-, meso-, metathoracic legs; C, coxa; F, femur; T, tibia; t, tarsus; ac, acrostichal setae; ad, anterodorsal; av, anteroventral; dc, dorsocentral setae; dv, dorsoventral; hm, postpronotal setae; npl, notopleural setae; pa, postalar setae; pd, posterodorsal; pm, presutural supra-alar setae; ppl, proepisternal setae; pv, posteroventral; sa, postsutural supra-alar setae; sr, presutural intra-alar setae; ♂ = male; ♀ = female.

TAXONOMIC PART

Family DOLICHOPODIDAE Latreille, 1809

Genus **CORINDIA** Bickel, 1986

Corindia Bickel, 1986: 137

Type species. *Corindia major* Bickel, 1986.

DIAGNOSIS — Subfamily characters of Medeterinae: antennal scape bare; dorsal postcranium strongly concave; posterior mesoscutum distinctly flattened, even slightly concave; femora II and III lacking anterior preapical setae; tibiae mostly bare of strong setae; vein M unbranched and lacking a flexion (*bosse alaire*) distad of dm-cu crossvein; hypopygium large and exerted, on peduncle formed by abdominal segment 7.

Generic characters of *Corindia*: body coloration mostly metallic green; eyes with short setulae between facets; ac present, biseriolate; only 1 sa present; coxa III with 2 lateral setae; femur II with strong posterior subapical seta; tibia II with

ad seta at 1/4 (pd absent); humeral crossvein complete; wing veins R4+5 and M parallel to apex; CuAx ratio > 0.5, *i.e.*, dm-cu relatively close to posterior margin of wing; anal vein weakly present to margin; hypandrium arising basoventrally from epandrium, and sometimes with flexion or indentation in distal third; hypopygial foramen left basolateral; phallus often with deep apicoventral notch; basal epandrial seta strong, curved, internal, not visible in lateral view; epandrial lobe with two strong setae arising from short basal collar; surstylus not strongly deflexed dorsad; ventral margin of cercus not conforming to dorsal surstylar margin; cercus with basal pilose mound from which distolateral arm with long setae projects; female oviscapt broad, with segment 9+10 bearing with 2 pairs of dorsal peg-like spines.

REMARKS — *Corindia* comprises nine Australian species (Bickel 1986) and three Afrotropical species, from Congo (Kinshasha) and Gabon (Grichanov 1998). In addition to the three Melanesian species described here, I also have seen a number of undescribed species from the Neotropical region. The genus is probably diverse and widespread, especially in the Southern Hemisphere and tropical regions.

Little is known of the habits of adult Melanesian *Corindia*, except that most specimens have been taken in Malaise traps or by general sweep-net collecting. In Australia, adult *Corindia* are known to occur on the trunks of smooth-barked trees, and are a common component captured in tree trunk sticky traps. On tree trunks they display a stance similar to that of *Medetera*, a vertical upright posture, with the body leaning outwards so that the abdomen makes an angle with the surface (Bickel 1986). Nothing is known of the immature stages of *Corindia*.

The three new Melanesian species described below are close to the nine described Australian species: *C. australis*, *C. capricornis*, *C. collessi*, *C. cooloola*, *C. major*, *C. minor*, *C. nigricornis*, *C. robensis*, and *C. torresiana*. These twelve species essentially form a single species group, defined primarily by the overall shape of the cercus, comprising rounded basal mound from which projects a distolateral arm being elongate setae. The species differ among themselves in minor details of coloration and setation, and the shape and configuration of the epandrium, phallus, surstylus and cercus.

Three of the Australian species are confined to the tropical north, and *C. torresiana* was described from the Torres Strait that separates Australia from New Guinea. Therefore, it is not surprising to find *Corindia* in the Papuan region, and undoubtedly, more species await collection. New Caledonia possibly obtained its fauna via dispersal along the “stepping stone” archipelago of islands from New Guinea (*i.e.* the Bismarck Archipelago, Solomon Islands, and Vanuatu to New Caledonia). Although *Corindia* is not known from the Solomon Islands and Vanuatu, these island groups are very poorly studied for small Diptera. However, the Fiji Islands further east are much better collected and studied, and *Corindia* is not known to occur there.

KEY TO MALES OF MELANESIAN *CORINDIA*

1. Antenna entirely dark brown; legs mostly brown; mesonotum and scutellum mostly metallic blue-green; epandrium elongate subrectangular (Figure 1c); phallus clavate and with ventral subapical notch; surstylus elongate and only shallowly cleft apically, with longer outer arm upcurved apically, distad of median arm; cercus with elongate curved distolateral arm bearing two apical setae and single subapical seta (New Ireland) ..
..... *Corindia mulleri* n. sp.
– At least antennal scape and pedicel yellow or red-yellow; at least tibiae and tarsi mostly yellow; colour of mesonotum and scutellum various; epandrium stouter, short subrectangular **2**
2. Thorax: mesonotum and scutellum dark metallic blue-green with violet reflections; hypopygium (Figure 1a); phallus greatly expanded and clavate apically; surstylus with longer outer arm bearing three long setae along ventral margin; cercus with distolateral arm bearing two apical setae (New Caledonia)
..... *C. amieuensis* n. sp.
– Mesonotum anteriorly dark metallic blue with violet reflections, but becoming brownish posteriad, with

humeral callus and scutellum yellowish; hypopygium (Figure 1b): phallus not expanded apically; surstylus with longer outer arm bearing two long setae along ventral margin; cercus elongate, with distolateral arm bearing three subapical setae and minute apical seta; (New Caledonia) *C. flaviscuta* n. sp.

SPECIES DESCRIPTION

All three species below share the following characters, which will not be repeated in the individual descriptions:

Head: pair of strong vertical and ocellar setae present; face violet and with longitudinal striae; eyes well-separated, anterior facets along face enlarged; first flagellomere rounded subrectangular; arista about 1.5x head height; lower postorbitals whitish, upper postorbitals black.

Thorax: five dc present which decrease in size anteriorly; one strong pa, one strong sa, one sr, one hm and 2 npl; anterior slope of mesonotum with field of some 20 short black setulae, extending from humeral callus to dc band; scutellum with one pair of strong median setae and one pair short of weak lateral hairs.

Wing: R1 joins the costa near 1/3; R₄₊₅ and M subparallel to apex; CuAx ratio: 0.9; lower calypter pale yellow with white hairs, halter pale yellow.

Abdomen: epandrial setae curved and positioned internally near base of epandrium; epandrial lobe as short peduncle and bearing two elongate setae.

Corindia amieuensis Bickel, n. sp.

Figure 1a

TYPE MATERIAL — Holotype: New Caledonia, ♂; paratypes, 6 ♂, 5 ♀, Prov. Sud, Reserve Col d'Amieu, 7.5 km NW of Sarraméa, 21.585°S 165.819°E, 303 m, 7-22.XII.2000, Malaise trap, DW Webb, EI Schlinger & ME Irwin; paratype, ♀, same but 9-14.XI.2000 (♂ holotype, and ♂ and ♀ paratypes deposited MNHN; remaining paratypes deposited INHS).

OTHER MATERIAL EXAMINED — New Caledonia: ♂, Prov. Nord., Mt. Mandjéla, 5 km WSW Puébo, 20.397°S 164.528°E, 720 m, 27.XI - 8.XII.2000, EI Schlinger & ME Irwin (INHS).

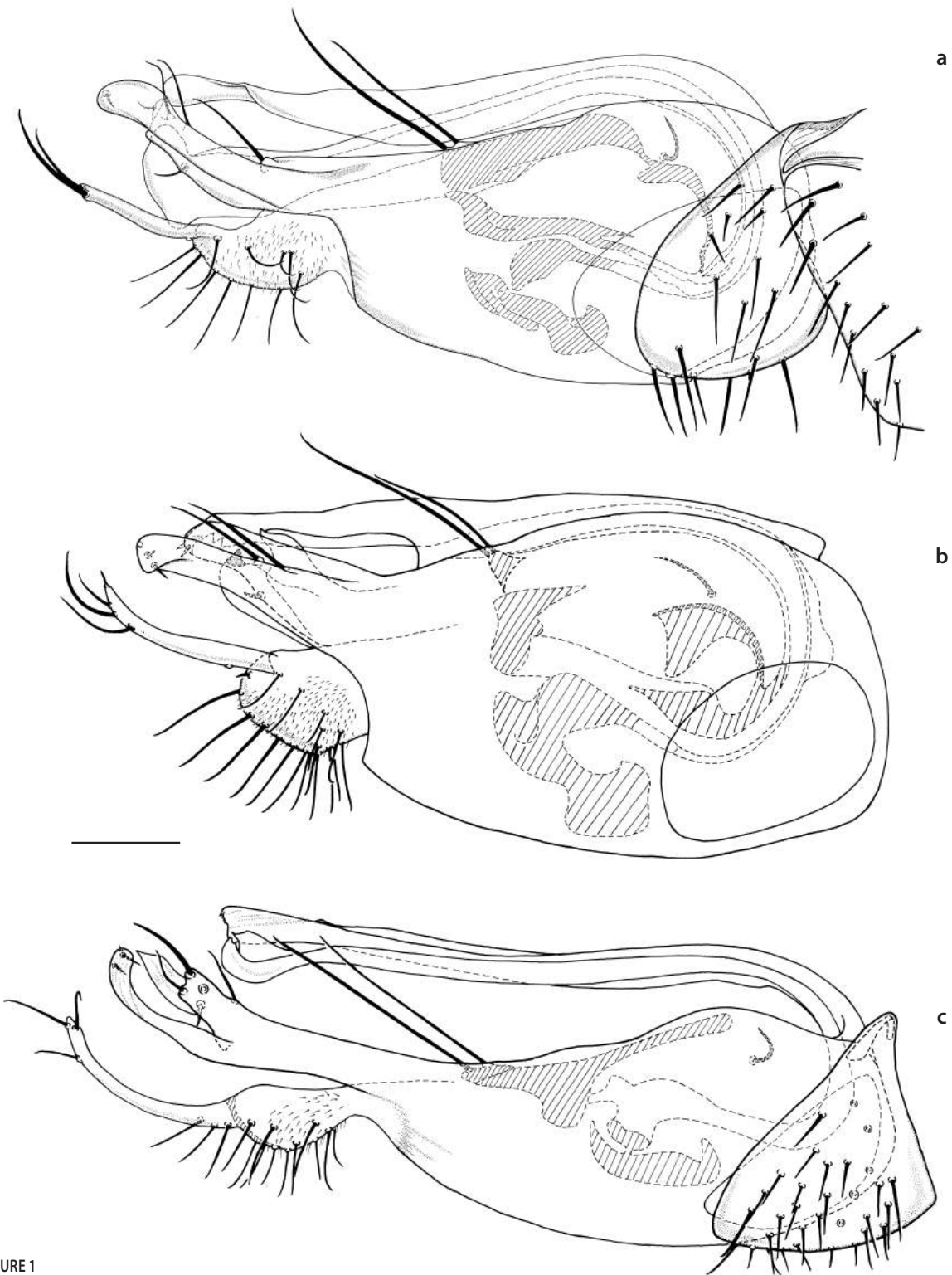
DESCRIPTION — *Male*. Length 2.5 - 2.6 mm; wing: 2.7 x 0.9 mm.

Head. Setae brown with yellowish reflections; vertex blue violet; palp dark brown with black short setulae and apical seta; proboscis brown; scape and pedicel yellowish, first flagellomere mostly dark brown.

Thorax. Mesonotum and scutellum dark metallic blue with violet reflections; setae dark brown; ac short biserial, approximately 10 pairs.

Legs. Coxae brown; trochanters and extreme base of femora yellow, with remainder of femora brown until apex; femoral "knees", tibiae and tarsi yellow; coxal vestiture whitish although stronger setae appear yellowish; CI with short anterior setae and some stronger distolateral setae; CII with short anterior setae and 2 stronger anterolateral seta; CIII with strong lateral seta at 1/3 and shorter lateral seta at 2/3; I: 3.3; 2.9; 1.5/ 0.8/ 0.3/ 0.3/ 0.3; FI with 2 short posterior setae in basal fifth, remainder of leg bare of major setae; II: 3.7; 3.6; 1.5/ 1.0/ 0.7/ 0.5/ 0.4; FII with subapical pv seta; TII with strong ad seta at ¼, and with strong apicoventral seta; III: 4.3; 4.4; 0.8/ 1.6/ 0.6/ 0.4/ 0.3; leg III bare of major setae.

Abdomen. Tergum mostly brown; terga 2-7 brown with metallic blue green reflections; vestiture brown with yellowish reflection; terga with longer seta near margins and otherwise covered with short setae; sterna brownish; sternum 8 brown; epandrium mostly dark brown, but with hypandrium, cercus and surstylus yellow; hypopygium (Figure 1a): epandrium subrectangular; hypandrium elongate, with angular flexion near 7/8; phallus greatly expanded and clavate apically; surstylus deeply cleft distally, with longer outer arm bearing three long setae along ventral margin, and overlapping median arm with single dorsal seta; cercus comprising rounded setose basal mound from which distolateral arm projects bearing two apical setae.

**FIGURE 1**

Hypopygium, left lateral. **a**, *Corindia amieuensis* n. sp.,
b, *C. flaviscuta* n. sp., **c**, *C. mulleri* n. sp. Scale bar = 0.1 mm.

Female: similar to male except as noted: face wider; abdominal terga 2 and 3 yellow laterally, and dark brown dorsally with some yellow areas near dorsal midline; sterna 3-5 mostly yellow.

REMARKS — *Corindia amieuensis* is known from two sites, Col d'Amieu in Province Sud and Mt. Mandjélia in Province Nord, New Caledonia.

Corindia flaviscuta Bickel, n. sp.

Figure 1b

TYPE MATERIAL — Holotype: New Caledonia, ♂, paratype, ♂, Prov. Sud, Réserve Col d'Amieu, 7.5 km NW of Sarraméa, 21.585°S 165.819°E, 303 m, 7-22.XII.2000, Malaise trap, DW Webb, EI Schlinger & ME Irwin; paratype, ♂, same but 25.XI-7.XII.2000 (♂ holotype deposited MNHN; remaining paratypes deposited INHS).

DESCRIPTION — **Male.** Length 2.6 mm; wing: 2.8 x 1.0 mm.

Head. Setae brown with yellowish reflections; vertex blue violet; palp dark brown with black short setulae and apical seta; proboscis yellow; scape and pedicel yellow, first flagellomere mostly dark brown, yellowish near base.

Thorax. Anterior mesonotum dark metallic blue with violet reflections, but becoming brownish posteriad, with thoracic angles just anterolaterad of scutellum and humeral callus yellowish; scutellum yellowish, but infuscated at base adjacent to mesonotum; setae dark brown; ac short biseriate, approximately 10 pairs.

Legs. Coxae mostly brown; trochanters and extreme base of femora yellow, with remainder of femora brown until distal third; distal third of femora, tibiae and tarsi yellow; coxal vestiture whitish; CI with short anterior setae and some stronger distolateral setae; CII with short anterior setae and 2 stronger anterolateral seta; CIII with strong lateral seta at 1/3 (stronger) and 2/3; I: 3.8; 3.0; 1.5/ 0.8/ 0.3/ 0.3/ 0.3; leg I bare of major setae; II: 4.1; 4.0; 1.8/ 1.2/ 0.8/ 0.6/ 0.4; FII with subapical pv seta; TII with strong ad seta at 1/4 and with strong av seta; III: 4.2; 4.5; 0.8/ 1.7/ 0.8/ 0.4/ 0.3; FIII with dorsal crest of 4-5 short yellow setae in basal quarter.

Abdomen. Tergum mostly brown; terga 2-7 brown with metallic blue green reflections; vestiture brown with yellowish reflection; terga with longer setae near margins and otherwise covered with short setae; sterna brownish; epandrium mostly dark brown, but yellowish along ventral margin and apically; hypandrium, cercus and surstylus mostly yellow; hypopygium (Figure 1b): epandrium subrectangular; hypandrium elongate, without subapical angular flexion; phallus not expanded apically; surstylus deeply cleft distally, with longer outer arm bearing two long setae along ventral margin, and laterally overlapping median arm with short dorsal seta; cercus elongate, with rounded setose basal mound from which distolateral arm projects bearing three subapical setae and one minute apical seta.

Female. Unknown.

REMARKS — *Corindia flaviscuta* is also known only from Col d'Amieu and was collected together in the same trap with the closely related *C. amieuensis*. The specific epithet refers to its yellowish scutellum.

Corindia mulleri Bickel, n. sp.

Figure 1c

TYPE MATERIAL — Holotype: Papua New Guinea, ♂, New Ireland: Central area, base of Hans Meyer Range, 0-10 m, 4°25'00" S 152°58'00" E, 27.IX.2000, C. J. Muller (AMS).

DESCRIPTION — **Male.** length 2.7 mm; wing: 2.3 x 0.8 mm.

Head. Setae black; vertex, frons and face blue-violet; palp dark brown with yellowish setulae and apical seta; proboscis dark brown; antenna entirely dark brown to black.

Thorax. Entirely metallic blue-green with brownish pruinosity; setae dark brown; ac short biseriate, approximately 14 pairs.

Legs. Coxae, trochanters, femora and tibiae and remainder of legs entirely brown, although femora knees and base of tibiae yellowish; tarsi yellowish; coxal vestiture whitish; CI and CII with short anterior setae; CIII with strong lateral seta at 1/3 and 2/3 and two short hairs anteriorly; I: 3.0; 2.3; 1.2/ 0.7/ 0.4/ 0.3/ 0.4; leg I bare of major setae; II: 3.1; 3.0; 1.4/ 0.8/ 0.5/ 0.4/ 0.4; FII with short subapical pv seta; TII bare of major setae; III: 3.3; 4.0; 0.8/ 1.2/ 0.7/ 0.4/ 0.4; FIII with dorsal crest of 4-5 short yellow setae in basal quarter, and with short pale ventral setae, otherwise leg bare.

Abdomen. Terga and sterna metallic blue green; vestiture dark brown with yellowish reflection, and terga with longer setae near margins and otherwise covered with short setae; epandrium mostly dark brown, but yellowish along ventral margin and apically; hypandrium, cercus and surstylus mostly yellow; hypopygium (Figure 1c): epandrium elongate subrectangular; hypandrium elongate, with angular flexion near 7/8; phallus slightly expanded apically, clavate and with ventral subapical notch; surstylus elongate and only shallowly cleft apically, with longer outer arm upcurved apically, distad of median arm, and bearing short subapical setae; median surstylar arm with median blade-like arm and with strong and weak apical setae; cercus comprising rounded setose basal mound from which elongate curved distolateral arm projects bearing two apical setae and single subapical seta.

Female. Unknown.

REMARKS — *Corindia mulleri* is known only from lowland New Ireland, an island to the east of the New Guinea mainland. This species is named in honor of the lepidopterist and geologist Chris Muller, who has collected insects in many remote parts of the world.

ACKNOWLEDGMENTS

Hannah Finlay drew the figures. Igor Grichanov provided specimens of Afrotropical *Corindia* for examination. I would like to thank the respective curators of the following institutions for information and the loan of specimens: (AMS) Australian Museum, Sydney, D. Britton. (INHS) Illinois Natural History Survey, Champaign, Illinois, C. Favret. (MNHN) Muséum national d'Histoire naturelle, Paris, C. Daugeron. (QMB) Queensland Museum, Brisbane, C. Burwell.

REFERENCES

- BICKEL D. J. 1986 — *Thrypticus* and an allied new genus, *Corindia* from Australia (Diptera: Dolichopodidae). *Records of the Australian Museum* 38: 135-151.
- BICKEL D. J. 2009 — Family Dolichopodidae, with annotated key to the New World genera, in BROWN, B. V. *et al.* Manual of Central American Diptera: volume 1, NRC Press, Ottawa, Ontario, Canada: 671-694.
- BICKEL D. J. & HERNÁNDEZ M. C. 2004 — Neotropical *Thrypticus* (Diptera: Dolichopodidae) reared from water hyacinth, *Eichhornia crassipes*, and other Pontederiaceae. *Annals of the Entomological Society of America* 97: 437-449. <http://iris.esa.catchword.org/freepdfs/00138746/v97n3s8.pdf>
- GRICHANOV I. Y. A. 1998 — Three new Afrotropical species of the Australian genus *Corindia* Bickel (Diptera: Dolichopodidae). *International Journal of Dipterological Research* 9(3): 191-194.

***Pindaia* (Diptera: Dolichopodidae) a new genus from New Caledonia and Australia**

Daniel J. Bickel

Australian Museum, 6 College Street, Sydney, NSW 2010 Australia
danb@austmus.gov.au

ABSTRACT

The genus *Pindaia* (Diptera: Dolichopodidae: Medeterinae) is described with three new species, *P. dispersia* from New Caledonia, *P. bellangrensis* and *P. enoggera* from eastern Australia, and an undescribed species represented by a female from the Papua New Guinea Highlands. A major diagnostic feature of *Pindaia* is the arista in a subapical lateral position on the first flagellomere, a character shared by the western Palaearctic medeterine genus *Cyrturella* Collin, as well as some members of the subfamily Achalchinae. Other diagnostic characters of *Pindaia* include the unmodified male segment 7 of the male, where both tergum and sternum are well developed and not prolonged or narrowed with respect to each other, and veins R_{4+5} and M are slightly bowed with respect to each other in the distal third of the wing.

RÉSUMÉ

***Pindaia* (Diptères : Dolichopodidae), un nouveau genre de Nouvelle-Calédonie et d'Australie.**

Le genre *Pindaia* (Diptères : Dolichopodidae: Medeterinae) est décrit ainsi que trois nouvelles espèces, *P. dispersia* de Nouvelle-Calédonie, *P. bellangrensis* et *P. enoggera* de l'est de l'Australie, et une espèce non décrite représentée par une femelle originaire des Hautes Terres de Papouasie-Nouvelle-Guinée. Un trait diagnostique majeur de *Pindaia* est l'arista en position latérale subapicale sur le premier flagellomère, un caractère partagé par le genre de medeterine paléarctique occidental *Cyrturella* Collin, ainsi que certains membres de la sous-famille des Achalchinae. Les autres caractères diagnostiques de *Pindaia* comprennent le segment 7 non modifié du mâle, où le tergum et le sternum à la fois sont bien développés et ne se prolongent pas ou sont rétrécis par rapport à l'autre et les nervures R_{4+5} et M sont légèrement inclinées par rapport à l'autre dans le tiers inférieur de l'aile.

INTRODUCTION

While sorting mass samples of Australasian Dolichopodidae, I occasionally found specimens of the new genus treated here and would tag them as “miscellaneous Medeterinae”. Since I found so few specimens, they were always set aside for future study. Recently, while studying all the odd and “leftover” taxa that had accumulated, I noted the similarity of New Caledonian and Australian specimens and determined that they should comprise a new genus, *Pindaia*, described here.

This is the first of five new genera of Australasian Medeterine awaiting description. Although collected by various methods, some of the new taxa are known only from tree trunk sticky traps. These traps are particularly efficient in capturing specimens that rest on vertical surfaces, a characteristic medeterine life habit.

MATERIALS AND METHODS

Drawings of genitalia were made with a camera lucida. The left lateral view of the hypopygium or male genital capsule is illustrated for most species. In describing the hypopygium, ‘dorsal’ and ‘ventral’ refer to morphological position prior to genitalic rotation and flexion. Thus, in figures showing a lateral view of the hypopygium, the top of the page is morphologically ventral, while the bottom is dorsal.

Wing length is the distance from the wing base to apex, and wing width is measured from the junction of R1 with the costa to the opposite side of the wing, perpendicular to the wing’s long axis. The CuAx ratio is the length of the m-cu crossvein/ distal section CuA1. The position of features on elongate structures such as leg segments is given as a fraction of the total length, starting from the base. The relative lengths of the podomeres are representative ratios and not measurements, and are given for each leg in the following formula and punctuation: trochanter + femur; tibia; tarsomere 1/ 2/ 3/ 4/ 5. The following abbreviations and terms are used: I, II, III: pro-, meso-, metathoracic legs; C, coxa; T, tibia; F, femur; ac, acrostichal setae; ad, anterodorsal; av, anteroventral; dc, dorsocentral setae; dv, dorsoventral; hm, postpronotal setae; npl, notopleural setae; pa, postalar setae; pd, posterodorsal; pm, presutural supra-alar setae; ppl, proepisternal setae; pv, posteroventral; sa, postsutural supra-alar setae; sr, presutural intra-alar setae; t, tarsus; t1-5, tarsomeres 1 to 5. Text symbols ♂ = male, ♀ = female.

TAXONOMIC PART

Family DOLICHOPODIDAE Latreille, 1809

PINDAIA Bickel n. gen.

Type species. *Pindaia dispersia* Bickel, n. sp.

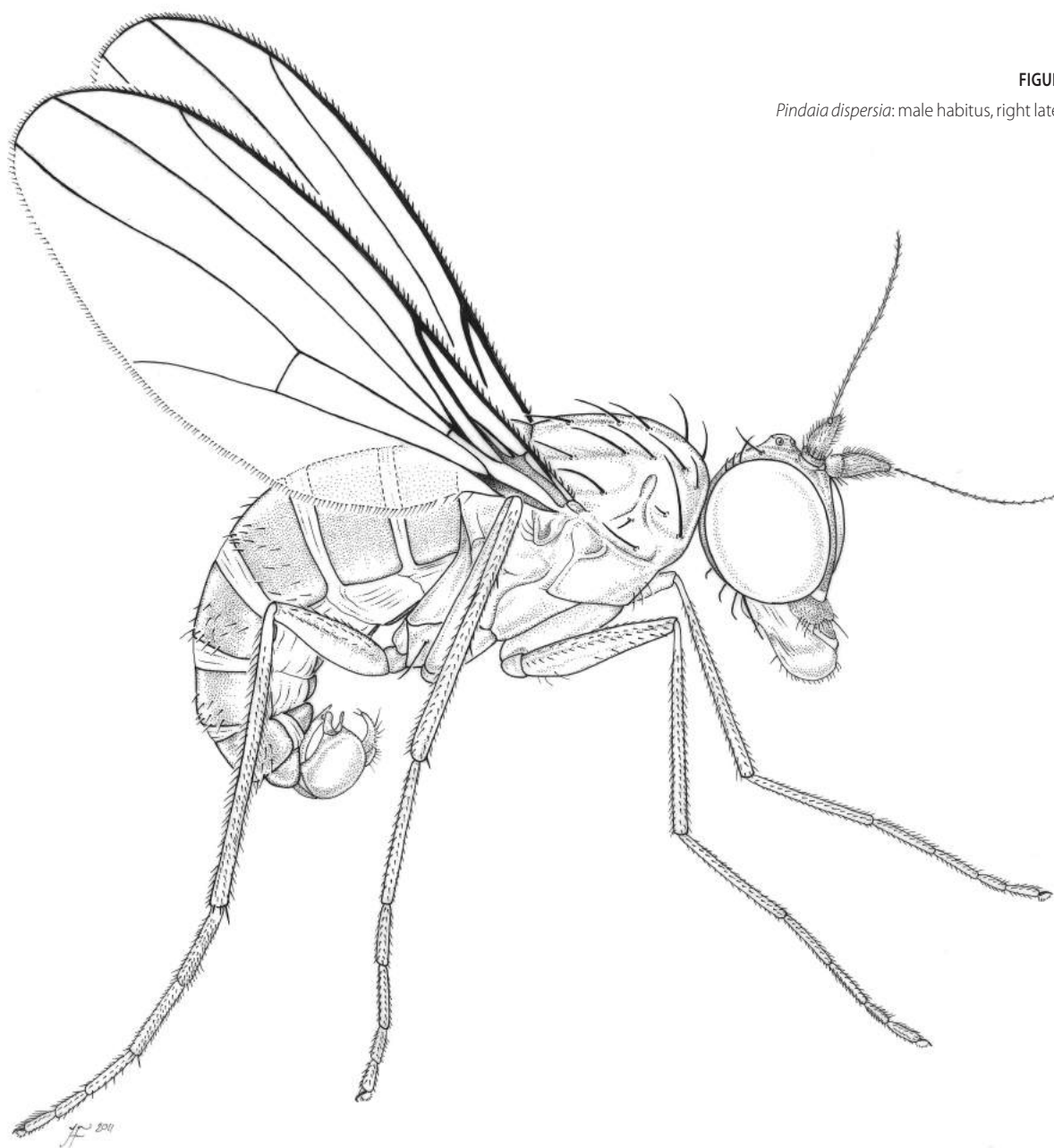
ETYMOLOGY — *Pindaia* is from “Pindai,” a place name of indigenous origin on the western coast of New Caledonia, a collecting site for the genus. The gender is feminine.

DIAGNOSIS — Subfamily characters of Medeterinae (see Key).

Generic characters of *Pindaia*: body length: 1.5-2.2 mm (habitus, Figure 1).

Head. Long and often slightly curved seta as ventralmost of postorbital series; relatively short vertical and diverging ocellar setae; face and clypeus parallel sided with eyes narrowly separated in male, wider in female; eye facets uniform and with tiny white setulae between facets; proboscis rather prolonged; first flagellomere oblong; arista arising subapically on the lateral surface of first flagellomere (Figure 2). laterad of proboscis.

FIGURE 1

Pindaia dispersia: male habitus, right lateral.

Thorax. ac totally absent; 5 strong dc present, slightly decreasing in size anteriorly; 1 strong pa, only 1 sa, 0 sr, 1 strong hm, 1 pm, 2 npl; 2 strong median scutellars, laterals absent; proepisternum with 1-3 ppl setae ventrad of anterior spiracle.

Legs. Coxa III with lateral seta at $\frac{1}{2}$; legs bare of major setae. Wing: vein R_{2+3} ending in costa near apical $\frac{4}{5}$; R_{4+5} and M more or less parallel beyond crossvein dm-cu, but distinctly bowed before reaching apex, with M ending slightly behind wing apex; CuAx ratio near 0.3.

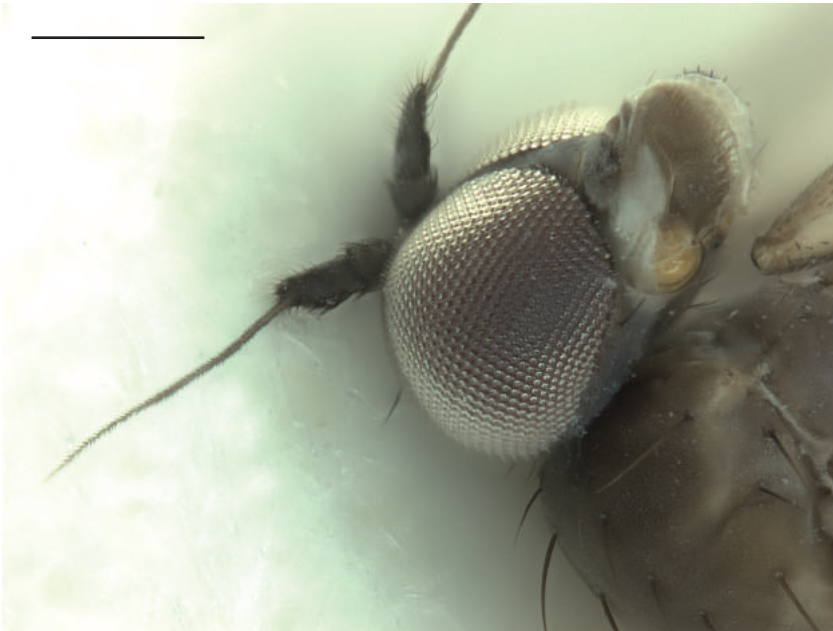


FIGURE 2

Pindaia dispersia, male head,
right ventral.

Abdomen. Terga 1-6 mostly bare but with some short setulae near posterior margins; unmodified; segment 7 bare, with tergum and sternum each well developed and not prolonged with respect to each other; hypopygia (Figures 2a-c); epandrium rounded subrectangular; epandrial seta not evident basally or internally; hypandrium as broad hood enclosing most of phallus; phallus sometimes sinuate; epandrial lobe enlarged and laterally flattened, and bearing two distal setae; cercus often short and lobate; oviscapt broad, with segment 9+10 bearing with 2 pairs of apical peg-like setae.

REMARKS — The genus *Pindaia* comprises three new species, *P. dispersia* from New Caledonia, and *P. bellangrensis* and *P. enoggera* from southeastern Australia. Based on the genus' distinctive antenna and venation, I have seen isolated females, undoubtedly representing an undescribed species of this genus, from Simbu Province, montane Papua New Guinea, with elevations around 2400 m (♀, Papua New Guinea, Kerowagi, 25.iii.1964, D.H. Colless, ANIC).

This is not the place to discuss the phylogenetic relationships of *Pindaia*, not the least because so little is known of the highly diverse subfamily Medeterinae. Many more genera await description, from both the recent fauna and the highly diverse Baltic amber fauna of Eocene-Oligocene age. And although many genera fit into a generalized concept of the subfamily Medeterinae as presented in the Diagnosis and Key, a complex range of male postabdominal configurations exists among these genera. The Medeterinae as a whole needs to be re-examined, and possibly reconfigured with the addition of new subfamilies.

MORPHOLOGY — The distinctive morphological characters that help define *Pindaia* are discussed below.

Lateral subapical arista. The most diagnostic feature of *Pindaia* is the arista arising from a lateral subapical position on the first flagellomere (Figure 2). This gives the visual impression of the arista being bent near its base, and once seen is readily recognized. In most other Medeterinae, the arista is either apical or *dorsally* subapical on the first flagellomere. However, this character is shared by another medeterine, the enigmatic western European genus *Cyrturella* Collin. The single included species, *C. albosetosa* (Strobl), is tiny (body length ~1.0 mm), and is either rare in nature or overlooked by collectors because of its size. It is also rarely cited in the literature, with the best treatment being that of Parent (1938), under the preoccupied name *Cyrtura*. Although it also has a lateral subapical arista [said by Parent to be “*apicale*” in the

generic summary, and the relevant antennal illustration (fig. 909) mistakenly show the arista as apical, he describes the arista as “*subapicale*” in his species description], it differs significantly from *Pindaia* by having vein M converging towards R_{4+5} beyond crossvein dm-cu (similar to that of the genus *Medetera*), and by having the sternum of segment 7 reduced to narrow strip, both characters in contrast to *Pindaia*.

It should be noted that a laterally subapical arista also occurs in the dolichopodid genera *Achalcus* Loew and *Australachalcus* Pollet, both of the subfamily Achalcinae. This subfamily shows some similarity to the Medeterinae, notably by also having a posteriole flattened mesonotum.

Thoracic setation. *Pindaia* has a rather reduced thoracic setation. Both the ac setae and the lateral scutellar seta are totally absent, losses that commonly occur in other Medeterinae and other Dolichopodidae generally. However, of the presence of only one pa seta (two usually present) and the absence of sr setae (one usually present) are more unusual. Also of interest is the present of proepisternal setae, not common in Medeterinae.

Venation. The following venation is distinctive for *Pindaia*: veins R_{4+5} and M more or less parallel beyond crossvein dm-cu, but slightly bowed before reaching apex, with M ending just behind the wing apex. The crossvein dm-cu is positioned away from the margin, giving a relatively low CuAx ratio of 0.3.

Male postabdomen. Of particular interest in *Pindaia* is the relatively unmodified male segment 7 of the male, where both tergum and sternum are well developed (Figure 2c) and not prolonged or narrowed with respect to each other. This is undoubtedly the plesiomorphic state in the Medeterinae. In most other medeterine genera, the sternum and tergum are modified and prolonged, often with sternum 7 reduced to a narrow strip, and sometimes even partially fused with the tergum to form a prolonged peduncle that can be used to thrust the hypopygium out from the abdomen (e.g., see Bickel 1986a, b). Regarding the characters of the hypopygium, the epandrial lobes are laterally flattened and enlarged, with strong distally projecting setae, while in most other Medeterinae, the epandrial lobe is short and collar-like or pedunculate, and bearing two strong apical setae.

ECOLOGY AND BIOGEOGRAPHY — *Pindaia* is associated with mixed rainforest and mesic sclerophyll forest habitats in New Caledonia and southeastern Australia. In New Caledonia these forests are regarded as predominately Gondwanan in origin (Mueller-Dombois & Fosberg 1998). In southeastern Australia, they comprise subtropical and temperate rainforest formations, also known for a predominance of Gondwanan floristic elements (Kitching *et al.* 2010).

Pindaia is also known from the Highlands of Papua New Guinea, at some 2400 m, which also suggests a Gondwanic connection with Australia. Hope (1996) noted that based on pollen, *Nothofagus* has been in New Guinea since the late Miocene, and that the cool moist climate, that these trees require, suggests a mid-Tertiary lowland biotic connection between Australia and proto-New Guinea. Subsequently, as the Australian Plate pushed northward into the tropics, the New Guinea mountains rose, and the overall climate became warmer, *Nothofagus* and other Gondwanan biota would have tracked the cool moist conditions higher into the mountains, and subsequently become disjunct from their temperate Australian congeners.

It must be remembered that *Pindaia* is only known from few specimens and is rarely collected. The genus might be more widely distributed and occur elsewhere in Australia or even in the Melanesian archipelagos east of New Guinea. Therefore, it is premature to comment extensively on the biogeographical history of *Pindaia*, except to say it has an *apparent* Gondwanan distribution encompassing New Caledonia, southeastern Australia and montane New Guinea.

KEY TO MALES OF THE SPECIES OF *PINDAIA* (DOLICHOPODIDAE)

[I have included the Palearctic genus *Cyrturella* in this key to provide comparison with *Pindaia*, for use in any future world generic key to Medeterinae.]

1. Dorsal postcranium strongly concave; posterior mesoscutum distinctly flattened, even slightly concave; femora II and III lacking anterior preapical setae; antennal scape bare; tibiae mostly bare of strong setae; vein M unbranched and lacking a flexion (*bosse alaïre*) distad of dm-cu crossvein; hypopygium usually large and

- exserted, often on peduncle formed by abdominal segment 7 (Medeterinae) **2**
 – Without this combination of characters other Dolichopodidae
- 2.** Arista arising subapically on lateral side of first flagellomere; propleuron ventrad of anterior spiracle with at least one seta; ventralmost seta of postocular series elongate and projecting; CuAx ratio close to 0.3 **3**
 – Arista arising apical on first flagellomere, or if subapically, than always dorsally subapical; propleuron rarely with strong setae; ventralmost seta of postocular series rarely outstanding; other characters variable
 other Medeterinae
- 3.** Veins R4+5 and M more or less parallel beyond crossvein dm-cu, but distinctly bowed before reaching apex, with M ending slightly behind wing apex; body length > 1.5 mm; ac totally absent; segment 7 with tergum and sternum each well developed and not prolonged or modified with respect to each other (e.g., Fig 2c); surstyli short and wide, less than half length of epandrium (New Caledonia, Australia, Papua New Guinea) *Pindaia* n. gen. **4**
 – Vein M converging towards R4+5 beyond crossvein dm-cu, with M joining margin anterior of wing apex; body length 1.0 mm; with 1-2 weak setae along anterior slope of ac row; sternum of segment 7 reduced to narrow strip, with tergum greatly enlarged; surstyli elongate and narrow, more than two-thirds length of epandrium (western Europe) *Cyrturella* Collin [single species, *C. albosetosa* (Strobl)]
- 4.** Body length 1.5-1.6 mm; proepisternum with single seta; femur III brown to dark brown; epandrial lobe broad and positioned basally with short basal pedunculate seta, and elongate apical pedunculate seta (Australia) **5**
 – Body length: 2.1-2.2 mm; proepisternum with 2-3 short setae; femora and tibiae mostly dull yellow; hypopygium (Figure 2c); epandrial lobe enlarged, positioned near surstylus, and bearing two distal setae; surstylus basally with two short pedunculate setae, and distally with two strong curved dorsal setae and strong median subapical seta (New Caledonia) *P. dispersia*
- 5.** Surstylus with apical U-shaped excavation, forming two thick arms, dorsal arms with apical tooth-like seta, and ventral arm with curved setae as figured (Figure 2a) *P. bellangrensis*
 – Surstylus with dorsal surstylar arm pedunculate and bearing two elongate setae which project well distad of surstylus (Figure 2b) *P. enoggera*

Pindaia dispersia n. sp.

Figures 1, 2, 3c

TYPE MATERIAL — Holotype male: New Caledonia, Province Sud, Rivière Bleue, Kaori Géant, 22°06'S 166°39'E, 210 m, 11.xi.2000, pyrethrum spray on trunks and logs, G. Monteith (QMB, deposited MNHN).

OTHER MATERIAL EXAMINED — New Caledonia: Province Nord: ♂, Presqu'île de Pindai, 2.5 km WSW Népoui, 21°22.968'S 164°58.421'E, 45 m, 17-22.xi.1998, Malaise trap in coastal forest, M.E. Irwin & S. Wright (INHS); 4 ♂, Forêt Nord, site 2, 22°19'S 166°55'E, rainforest, 22.xii.2004-8.i.2005, Malasia trap, C. Burwell & S. Wright (QMB). Province Sud: 2 ♂, Pic du Pin, 22°15'S 166°49'E, 250m, Malaise trap site 1, rainforest, 25.xi-23.xii.2004; C. Burwell & S. Wright (QMB); 2 ♂, Pic du Grand Kaori, site 1, 22°17'S 166°53'E, 250 m, Malaise trap site 4, 22.xi-22.xii.2004, 22.xii.2004 - 12.i.2005, C. Burwell & S. Wright (QMB); 2 ♂, Cap Ndoua, site 2, 22°23'S 166°55'E, 50 m, 29.xi - 21.xii.2004, 21.xi.2004 - 8.i.2005, Malaise trap, C. Burwell & S. Wright (QMB). ♂, Rivière Bleue, Parc 7, 170 m, Malaise trap, forêt humide sur alluvions, 28.iii - 3.iv.1987, L. Bonnet de Larbogne, J. Chazeau & S. Tillier (MNHN).

DESCRIPTION — *Male*. Body length: 2.1 – 2.2 mm; wing: 2.0 x 0.7 mm.

Head. Postorbitals short and rather widely spaced in single row, with ventral setae whitish and dorsal ones dark brown; long, slightly curved and projecting dark brown seta ventralmost of postorbital series; vertex, frons and face metallic

black and covered with dense grey pruinosity; setae brown with yellowish reflections; pairs of relatively short vertical and diverging ocellar setae present; postvertical setae weak, about half as long as verticals; face and clypeus parallel sided, with eyes narrowly separated; eye facets uniform and with tiny white setulae between facets; palp brown with grey pruinosity, and three short black setae; proboscis dark brown and rather prolonged; antenna black; scape bare, and subequal in length to pedicel; pedicel with ring of very short setae; first flagellomere oblong; arista arising subapically on the lateral surface of first flagellomere and with arista longer than head height; some weak ventral postcranial setae present, and with pair of strong white setae ventrad of occiput (mostly hidden from view).

Thorax. Mesonotum and scutellum mainly brown but with yellowish cuticle on scutellum, humeral area, and near sutures, and covered with dusting of grey pruinosity; mesonotum with posterior third distinctly flattened and bordered laterally by two posteriormost dc setae; all thoracic setae black; ac absent; 5 strong dc present, slightly decreasing in size anteriorly; 1 strong pa, only 1 sa, 0 sr, 1 strong hm, 1 pm, 2 npl; median scutellar strong, laterals absent; proepisternum with 2-3 short setae.

Legs. CI light brown; CII and CIII mostly dark brown, all trochanters, femora, tibiae and tarsi dull yellow, with femora slightly infuscated along dorsal surface; vestiture black; CI with 4 short anteroapical distolateral setae; CII with some short anterolateral setae; CIII with lateral seta at $\frac{1}{2}$; legs bare of major setae; I: 2.4; 2.2; 1.4/ 0.8/ 0.6/ 0.4/ 0.3; II: 2.5; 3.4; 1.7/ 0.7/ 0.5/ 0.4/ 0.3; TII with circlet of very short preapical setae: dorsal, ad, pd, pv, and av; III: 3.4; 3.8; 1.1/ 0.9/ 0.6/ 0.4/ 0.3; TIII with very short preapical ad and ventral setae.

Wing. Membrane hyaline, vein R_{2+3} ending in costa near 4/5; R_{4+5} and M more or less parallel beyond crossvein dm-cu, but distinctly bowed before reaching apex, with M ending slightly behind wing apex; CuAx ratio: 0.3; lower calypter yellow with fan of pale yellow setae; halter dark brown.

Abdomen. Terga 1-6 mostly dark brown, and mainly bare, with some short setulae near posterior margins; sterna 1-6 also brown and unmodified; segment 7 with tergum and sternum bare, well developed and not prolonged with respect to each other; sternum 8 ovate and with some short setae, mostly along margins; hypopygium (Figure 2c) mostly dark brown but with yellowish hypandrium and surstylus, epandrium rounded subrectangular; basal epandrial seta not evident; hypandrium as broad hood enclosing most of phallus; phallus strongly sinuate; epandrial lobe enlarged and positioned near surstylus, and plate-like, and bearing two distal setae, surstylus basally with two short pedunculate setae, and distally with two strong curved dorsal setae and strong median subapical seta; cercus as short setose lobe.

Female. Unknown.

REMARKS — *Pindaia dispersia* is known from a number of lowland (< 300 m) sites throughout New Caledonia, hence the specific epithet, “*dispersia*”, from the Latin meaning “scattered”. It occurs in humid forest habitats, mostly rainforest, but also drier coastal forest.

***Pindaia bellangrensis* n. sp.**

Figure 3a

TYPE MATERIAL — Holotype male: Australia, New South Wales, Wilson River Reserve, 15 km NW of Bellangry, 31°12'S 152°28'E, 240 m, 16-19.xi.1998, yellow pans, wet side channels of river, D. Bickel (AMS – K364703).

OTHER MATERIAL EXAMINED — Australia: New South Wales: 2 ♂, Cockerawombeebea Creek, 23 km WNW of Bellangry, 31°11'S 152°22'E, 730 m, warm temperate rainforest, yellow pans, 14-15.i.1988, D. Bickel (AMS); ♂, Cockerawombeebea Flora Reserve, east of Creek, 800 m, warm temperate rainforest, sticky trap on *Polyscias elegans* trunk (Araliaceae), 16-19.xi.1998, D. Bickel (AMS); ♂, New England NP, Point Lookout, 30°29'S 152°25'E, 1400 m, 12.ii.1984, I.D. Naumann (ANIC).

DESCRIPTION — **Male.** Body length: 1.7-1.8 mm; wing: 1.8 x 0.7 mm. Similar to *P. dispersia* except as noted.

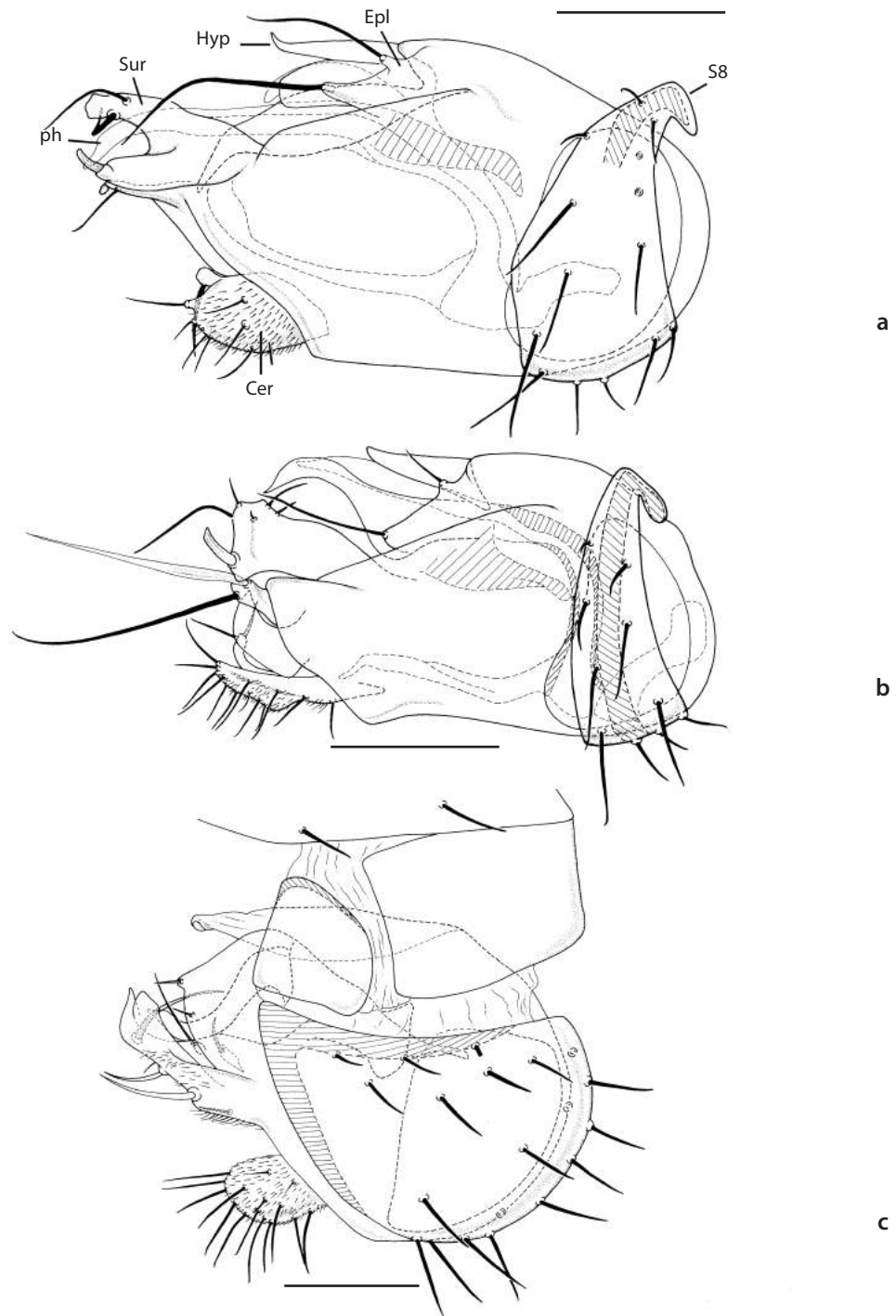


FIGURE 3

Male hypopygium, left lateral. **a**, *Pindaia bellangrensis*. **b**, *P. enoggera*. **c**, *P. dispersa*. Legend: Cer, cercus; Epl, Epandrial lobe; Hyp, hypandrium; Ph, phallus; Sur, surstylus; S8, sternum 8. Scale bar = 0.1 mm.

Head. Vertex, frons and face metallic black and covered with dense brown pruinosity; ventral postcranium with pair of long white distally curved setae ventrad of occiput, and reaching to base of proboscis.

Thorax. Dark brown with metallic blue-green reflections and with dusting of grey pruinosity; setae dark brown with yellowish reflections; proepisternum with only single long seta.

Legs. All coxae brown; FI yellowish, FII yellowish but infuscated dorsally, and FIII brown to dark brown; all tibiae and tarsi dull yellow; vestiture black; CI with short lateral and anteroapical setae; CII with some short anterolateral setae; CIII with lateral seta at $\frac{1}{2}$; legs bare of major setae; I: 2.1; 2.0; 1.1/ 0.6/ 0.4/ 0.3/ 0.3; II: 2.4; 2.7; 1.6/ 0.7/ 0.4/ 0.3/ 0.3; TII with circlet of very short preapical setae: dorsal, ad, pd, pv, and av; III: 3.4; 3.6; 1.0/ 0.9/ 0.5/ 0.4/ 0.3; TIII with very short preapical ad and ventral setae.

Wing. CuAx ratio: 0.3; lower calypter yellow with fan of dark brown setae; halter dark brown.

Abdomen. Terga 1-6 mostly dark brown; sterna 1-6 also brown and unmodified; segment 7 with tergum and sternum each well developed and not prolonged with respect to each other, and segment bare of setae; sternum 8 narrowly ovate and with some short setae; epandrium rounded subrectangular; hypandrium short, half length of epandrium, and with upcurved apex; phallus elongate; epandrial lobe broad and positioned basally, with short basal peduncular seta, and elongate apical pedunculate seta; surstylus with apical U-shaped excavation, forming two thick arms, dorsal arms with apical tooth-like seta, and ventral arm with curved setae as figured; cercus as short setose lobe.

Female. Unknown.

REMARKS — *Pindaia bellangrensis* is known from rainforest in northeastern New South Wales at elevations ranging from 240 m (subtropical rainforest) to 1400 m (cool temperate rainforest). Specimens have been collected on tree trunk sticky traps and yellow pans.

The specific epithet *bellangrensis* is from the town of Bellangry though which one drives to reaching the rainforests of the Hastings River drainage, in particular the abovementioned collecting sites at Wilson River and Cockerawombeebah Creek.

***Pindaia enoggera* n. sp.**

Figure 3b

TYPE MATERIAL — Holotype male: Australia, Queensland, paratypes ♂, ♀, Brisbane Forest Park, Ennoggera Creek & Scrub Rd crossing, 27°25'42" S 152°50'33"E, 200 m, 14-29.xi.1995, Malaise trap, mixed subtropical rainforest and *Eucalyptus*, M.E. Irwin (INHS, deposited QMB).

OTHER MATERIAL EXAMINED — Australia: New South Wales: ♂, 2 ♀, Wilson River Reserve, 15 km NW of Bellangry, 31°12'S 152°28'E, 240 m, 16-19.xi.1998, sticky traps on *Eucalyptus grandis* trunk, D. Bickel (AMS).

DESCRIPTION — **Male.** Body length: 1.5 – 1.6 mm; wing: 1.6 x 0.6 mm. Similar to *P. dispersia* except as noted.

Head. Vertex, frons and face metallic black and covered with dense brown pruinosity; ventral postcranium with pair of longer white setae ventrad of occiput.

Thorax. Dark brown with metallic blue-green reflections and with dusting of grey pruinosity; setae yellowish; proepisternum with only single long seta.

Legs. Coxae dark brown, legs II and III mostly dull yellow; FIII dark brown, TIII and tarsus III dull yellow; vestiture brownish; CI with short lateral and anteroapical setae; CII with some short anterolateral setae; CIII with lateral seta at $\frac{1}{2}$; legs bare of major setae; I: 2.0; 1.8; 0.9/ 0.6/ 0.4/ 0.2/ 0.2; II: 2.3; 2.8; 1.3/ 0.7/ 0.4/ 0.3/ 0.2; TII with circlet of very short preapical setae: dorsal, ad, pd, pv, and av; III: 2.5; 2.9; 0.7/ 0.9/ 0.5/ 0.3/ 0.2; TIII with very short preapical ad and ventral setae.

Wing. CuAx ratio: 0.3; lower calypter yellow with fan of pale yellow seta; halter yellowish with club infuscated.

Abdomen. Terga 1-6 mostly dark brown; sterna 1-6 also brown and unmodified; segment 7 with tergum and sternum each well developed and not prolonged with respect to each other, and segment bare of setae; sternum 8 narrowly ovate and with some short setae; epandrium rounded subrectangular; hypandrium short, half length of epandrium, and with upcurved apex; phallus elongate and sinuate; epandrial lobe broad and positioned basally, with short basal peduncular seta, and elongate apical pedunculate seta; ventral surstylar arm enlarged and clavate, and bearing toothlike seta; dorsal surstylar arm pedunculate and bearing two elongate setae which project well distad of surstylus; cercus elongate, with strong setae along dorsal surface, and with median curved peduncle bearing with two distal setae.

Female. Similar to male except as noted: face and clypeus slightly wider; setation and wing similar; oviscapt broad, with segment 9+10 bearing with 2 pairs of apical peg-like setae.

REMARKS — *Pindaia enoggera* is known from lowland (< 250 m) mixed subtropical rainforest and wet sclerophyll *Eucalyptus* forest along creeks in southeastern Queensland and northeastern New South Wales. This species is sympatric with *P. bellangrensis* at the Wilson River site. Specimens have been collected on tree trunk sticky traps and in Malaise traps.

The specific epithet is derived from “Enoggera” a place name of indigenous Australian origin and should be regarded as a noun in apposition.

ACKNOWLEDGMENTS

Hannah Finlay drew the figures and John Martin photographed Figure 2. Peter Dyte (Datchet, England) kindly provided specimens of *Cyrturella albosetosa*. Any reference to the repository of material cited in the text uses the institutional abbreviations designated below. I would like to thank the respective curators of these institutions for information and the loan of specimens: (AMS) - Australian Museum, Sydney; D. Britton, J. Resci. (ANIC) - Australian National Insect Collection, CSIRO, Canberra; D. Yeates. (INHS) - Illinois Natural History Survey, Champaign, Illinois; C. Favret, M. Irwin. (MNHN) - Muséum national d'Histoire naturelle, Paris; M. Baylac, C. Daugeron. (QMB) - Queensland Museum, Brisbane, C. Burwell.

REFERENCES

-
- | | |
|---|---|
| <p>BICKEL D. J. 1986a — <i>Atlaltia</i>, a new genus of Dolichopodidae (Diptera) from Australia. <i>Entomologica scandinavica</i> 17: 165-171.</p> <p>BICKEL D. J. 1986b — <i>Thrypticus</i> and an allied new genus, <i>Corindia</i>, from Australia (Diptera: Dolichopodidae). <i>Records of the Australian Museum</i> 38: 135-151.</p> <p>HOPE G. S. 1996 — History of Nothofagus in New Guinea and New Caledonia, in VELEN T. T., HILL R. S. & READ J. (eds). <i>The ecology and biogeography of Nothofagus forests</i>, Yale University Press, New Haven: 257-270.</p> | <p>KITCHING R.L., BRAITHWAITE R. & CAVANAUGH J. (eds) 2010 — <i>Remnants of Gondwana – A natural and social history of the Gondwana Rainforests of Australia</i>. Surrey Beatty & Sons, Baulkham Hills, NSW Australia, 551 p.</p> <p>MUELLER-DOMBOIS D. & FOSBERG F. R 1998 — <i>Vegetation of the Tropical Pacific Islands</i>. Springer-Verlag, New York, 733 pp.</p> <p>PARENT O. 1938 — <i>Diptères Dolichopodidae. Faune de France</i> 35. Lechevallier, Paris, 720 p.</p> |
|---|---|

The water bugs (Hemiptera-Heteroptera: Gerromorpha & Nepomorpha) of New Caledonia: Diversity, ecology and biogeographical significance

Jakob Damgaard ⁽¹⁾ & Herbert Zettel ⁽²⁾

⁽¹⁾ Laboratory of Molecular Systematics, Botanical Garden and Museum Natural History Museum of Denmark
Sølvgade 83 Opg. S, 1307 Copenhagen K. Denmark
JDamgaard@snm.ku.dk

⁽²⁾ International Research Institute of Entomology, Natural History Museum Vienna
Burgring 7, 1010 Vienna, Austria

ABSTRACT

The New Caledonian fauna of water bugs (Hemiptera-Heteroptera: Gerromorpha and Nepomorpha) is reviewed and presented in a check-list. The fauna is quite diverse with 35 described and several undescribed species. Approximately half of all species are endemic to the main island, Grande Terre, and surrounding islands and coral reefs. Despite its small size and isolated position, New Caledonia is inhabited by representatives of most families of semi-aquatic bugs (Gerromorpha) - Mesoveliidae, Hebridae, Hydrometridae, Hermatobatidae, Veliidae and Gerridae. The fauna of aquatic bugs (Nepomorpha) is less diverse and includes representatives of Belostomatidae, Corixidae, Notonectidae, Ochteridae and Gelastocoridae. Most species belong to widespread or even cosmopolitan genera such as *Mesovelvia*, *Hebrus*, *Hydrometra*, *Hermatobates*, *Microvelia*, *Rhagovelia*, *Halovelia*, *Xenobates*, *Halobates* and *Limnogonus* (Gerromorpha) and *Lethocerus*, *Sigara*, *Ochterus*, *Nerthra*, *Anisops*, *Enithares* and *Paraplea* (Nepomorpha). Many species are found only on surrounding islands while some are widely distributed in the western Pacific region and beyond. *Trichocorixa verticalis verticalis* Fieber, 1851 was probably introduced from eastern North America during the Second World War. Most New Caledonian species of Nepomorpha live in lentic and lotic freshwater habitats but some Gelastocoridae and Ochteridae live in moist terrestrial habitats. The majority of New Caledonian species of Gerromorpha are also found in lentic and lotic freshwater habitats, but as many as 36% of the species occur only in marine environments. Members of the mesoveliid genera *Austrovelia* and *Phrynovelia* are found in moist terrestrial environments on mountain tops and may be particularly interesting with respect to understanding the much debated historical biogeography of the area.

RÉSUMÉ

Les punaises aquatiques (Hemiptères-Hétéroptères : Gerromorpha & Nepomorpha) de Nouvelle-Calédonie : diversité, écologie et importance biogéographique.

La faune néo-calédonienne des punaises d'eau (Hemiptères-Hétéroptères : Gerromorpha et Nepomorpha) est examinée et présentée dans une liste. La faune est très diversifiée avec 35 espèces décrites et quelques espèces non décrites. Les espèces pour environ leur moitié sont endémiques à l'île principale, la Grande Terre et les îles environnantes et les récifs coralliens. Malgré sa petite taille et sa position isolée, la Nouvelle-Calédonie est habitée par des représentants de la plupart des familles de punaises semi-aquatiques (Gerromorpha) - Mesoveliidae, Hebridae, Hydrometridae, Hermatobatidae, Veliidae et Gerridae. La faune des punaises aquatiques (Nepomorpha) est moins diversifiée et comprend des représentants des Belostomatidae, Corixidae, Notonectidae, Ochteridae et Gelastocoridae. La plupart des espèces appartiennent à des genres répandus, voire cosmopolite comme *Mesovelia*, *Hebrus*, *Hydrometra*, *Hermatobates*, *Microvelia*, *Rhagovelia*, *Halovelia*, *Xenobates*, *Halobates* et *Limnogonus* (Gerromorpha) et *Lethocerus*, *Sigara*, *Ochterus*, *Nerthra*, *Anisops*, *Enithares* et *Paraplea* (Nepomorpha). De nombreuses espèces ne se trouvent que sur les îles environnantes tandis que d'autres sont largement distribuées dans la région du Pacifique occidental et au-delà. *Trichocorixa verticalis verticalis* Fieber, 1851 a probablement été introduite à partir de l'Amérique du Nord pendant la Seconde Guerre mondiale. La plupart des nouvelles espèces néo-calédoniennes de Nepomorpha vivent dans des habitats d'eau douce lenticues et lotiques mais certains Gelastocoridae et Ochteridae vivent dans des habitats terrestres humides. La majorité des nouvelles espèces néo-calédoniennes de Gerromorpha se trouve également dans les habitats d'eau douce lenticues et lotiques, mais autant que 36% des espèces sont présentes uniquement dans les milieux marins. Les membres des genres de mesoveliides *Austrovelia* et *Phrynovelia* se trouvent dans les milieux terrestres et humides sur les sommets des montagnes et peuvent être particulièrement intéressants pour comprendre la biogéographie historique de la région qui est actuellement débattue.

INTRODUCTION

The water bugs (Hemiptera-Heteroptera: Gerromorpha & Nepomorpha) comprise two relatively small but highly significant groups of mainly limnic insects (Schuh & Slater 1995; Polhemus & Polhemus 2008a). The Gerromorpha, or semi-aquatic bugs, include eight currently recognized families: Mesoveliidae ("pondweed bugs"), Hebridae ("velvet bugs"), Hydrometridae ("water measurers"), Hermatobatidae ("coral treaders"), Veliidae ("water crickets"), Gerridae ("water striders") and Paraphrynoveliidae and Macroveliidae (no common names) and is one of the best-studied heteropteran clades in terms of phylogeny, ecology, behavior, adaptation and fossil history (Andersen 1982; 1998; Spence & Andersen 1994; Damgaard 2008a, b). Most gerromorphans live on the surface of freshwater habitats such as lakes, ponds, rivers, and streams and feed on dead and drowning insects. However, some lineages are confined to moist terrestrial habitats while others have successfully adapted to a marine life (Andersen 1982; Spence & Andersen 1994). The Nepomorpha, or aquatic bugs, includes 13 currently recognized families: Nepidae ("water scorpions"), Belostomatidae ("giant water bugs"), Corixidae ("water boatmen"), Micronectidae ("pygmy water boatmen"), Ochteridae ("velvety shore bugs"), Gelastocoridae ("toad bugs"), Aphelocheiridae ("ground bugs"), Naucoridae ("creeping water bugs"), Notonectidae ("backswimmers"), Pleidae ("pygmy backswimmers") and Potamocoridae, Helotrephidae and Diaprepocoridae (no common names) (Chen *et al.* 2005; Polhemus & Polhemus 2008a). Most nepomorphans are predators in lentic and lotic freshwater habitats and are most prolific in marginal, benthic vegetation: a very small number of species, however, are found in marine environments (Scudder 1976) while members of the Gelastocoridae and Ochteridae are fully terrestrial (Schuh & Slater 1995). Water bugs are found in all the world's temperate, subtropical and tropical regions and even though most attention historically has been given to the rather uniform Holarctic fauna (Henry & Froeschner 1988; Aukema & Rieger 1995), recent research has increasingly focused on the highly diverse Australian (Andersen & Weir 2004a) and Malesian Regions (Chen *et al.* 2005).

New Caledonia is an island group in the southwestern Pacific on the margins of the Australian and Pacific continental plates approximately 1 300 km east of Queensland, Australia, and 1700 km north of New Zealand's North Island. The main island, Grande Terre (*ca* 16 000 km²), is very rugged and includes five mountain tops higher than 1 500 m a.s.l., with Mt. Panié (1 678 m) reaching the highest altitude. Surrounding Grande Terre are several smaller islands and reefs. The Loyalty Islands (Ouvéa, Lifou and Maré) are found 125 km north-east of the main island. The Isle of Pines lies immediately to its southern end while Îles Bélep is situated at its north. Several small, uninhabited islands are situated at increasing distances

east of Isle of Pines —Walpole (200 km), Deer (400 km), Matthew (630 km) and Hunter (600 km)— while 600 km west of Îles Bélep are the Chesterfield Islands. Freshwater habitats are in the form of streams, rivers and artificial lakes on the main island but canals, ditches and artificial ponds are found throughout the area. Grande Terre is surrounded by one of the largest barrier reefs in the world (second only to Australia's Great Barrier Reef), and the lagoon is accordingly rich in marine habitats including mangroves, estuaries and intertidal rock pools.

During the late Cretaceous (*ca* 80 million years ago (mya); McLoughlin 2001) the continental part of New Caledonia (mainly Grande Terre) separated from north-eastern Australia and drifted towards the northeast away from the continent. What happened next is central to vibrant discussions among geologists and researchers working with historical biogeography. While there is substantial geological evidence that the main island itself originated from the ancestral supercontinent Gondwana, but presence of ultramafic soils originating from the ocean floor and accumulation of deep-water sediments indicates that the island was inundated for at least 20 million years from the Paleocene to the late Eocene, and that the present land masses re-emerged probably 37 mya (Pelletier 2006). In accordance with its long period of isolation, New Caledonia is known for an extreme degree of endemism and is considered its own floristic region. The area includes taxa that have no close relatives, such as the nearly flightless Kagu (*Rhynochetos jubatus* Verraux & Des Murs 1860), the island's national bird and sole extant member of Rhynochetidae, which is considered to be sister group to the likewise monotypic Eurypygidae consisting of the Sunbittern (*Eurypyga helias*) from the Neotropical Region (Hackett *et al.* 2008). Another well-known example of an endemic of a high taxonomic level is *Amborella trichopoda* Baillon, 1873, the sole representative of Amborellaceae and considered to be the sister group to all other flowering plants (Drew *et al.* 2014). Undoubtedly, the area was originally inhabited by a tropical Gondwanan flora and fauna and even though many extant taxa have their closest relatives in surrounding areas, it is unlikely that such lineages represent survivors *in situ* but descend from ancestors that reached New Caledonia via long distance dispersal (Sanmartín & Ronquist 2004, Grandcolas *et al.* 2008, Muriénne 2009, Turner *et al.* 2013). The invertebrate fauna is still insufficiently known but includes many taxa of possible Gondwanan origin (*e.g.* water beetles, Balke *et al.* 2007a & b; Jäch & Balke 2010; harvestmen, Sharma & Giribet 2009 and centipedes, Edgecombe & Giribet 2009). Among the Hemiptera, there is also a significant degree of endemism and several presumably relictual lineages inhabit the islands. Most interesting is the presence of peloriidiids or moss-bugs (Hemiptera-Coleorrhyncha: Peloriidiidae), a small group of moss-feeding insects from temperate rainforests in New Zealand, Patagonia and Australia (including Tasmania and Lord Howe I.) (Evans 1981; Burckhardt 2009) and considered to be the sister group to Heteroptera (Wheeler *et al.* 1993; Ouvrard *et al.* 2000) (Figure 1). With respect to Heteroptera, New Caledonia is inhabited by some of the most plesiomorphic species in groups such as Enicocephalomorpha ("unique-headed bugs") (Štys 2008) and Cimicomorpha: Miridae ("plant bugs") (Cassis *et al.* 2003).

The first water-bug species from New Caledonia were recorded by Jean Xavier Hyacinthe Montrouzier (1820-1897), a French priest, explorer and natural historian, who described *Gerris luctuosa* (now *Limnogonus luctuosus*), *Hydrometra aculeata* and *Pelogonus dufourii* (now *Ochterus dufourii*) (Montrouzier, 1864). The results of subsequent surveys and revisions addressing the water-bug fauna were published by Distant (1914, 1920), Lundblad (1933, 1936), Brooks (1951), Lansbury (1968, 1970), Polhemus & Herring (1970a, b), Jansson (1982), Malipatil & Monteith (1983), Baehr (1989), Andersen & Weir (1999, 2000), Andersen & Polhemus (2003), Andersen & Cheng (2004) and Cassis & Silveira (2006) and much material has been collected during scientific expeditions to the area.

While Andersen & Weir (2004a), Larivière & Larochelle (2004), Chen *et al.* (2005), Nieser & Chen (2005) have reported on the neighboring areas in great detail, no comprehensive faunal survey has been carried out on New Caledonia since two almost identical papers published by Polhemus & Herring (1970a; b), which were based mainly on material collected in 1965 by the late Prof. Ferdinand Starmühlner of the University of Vienna, Austria.

Water bugs are known to have been present since the Mesozoic (Popov 1971; Andersen 1998; Popov & Bechly 2007; Damgaard 2008b) and due to their island-like habitats and often-limited dispersal abilities, they offer great potential for testing scenarios related to historical biogeography. Analytical biogeography depends on robust reconstructions of phylogenetic relationships, and such have recently been designed for Nepomorpha and Gerromorpha. These include a complete taxon sampling of families, and comparative analyses of morphological and molecular data sets (Hebsgaard

et al. 2004; Damgaard 2008a). The aims of the present study are to bring an updated checklist of the New Caledonian fauna of water bugs, to discuss the diversity in the light of the recent theories of phylogenetic relationships of Heteroptera, and to examine how relationships among aquatic and semi-aquatic bugs may contribute to the standing discussion of the historical biogeography of the New Caledonian flora and fauna.

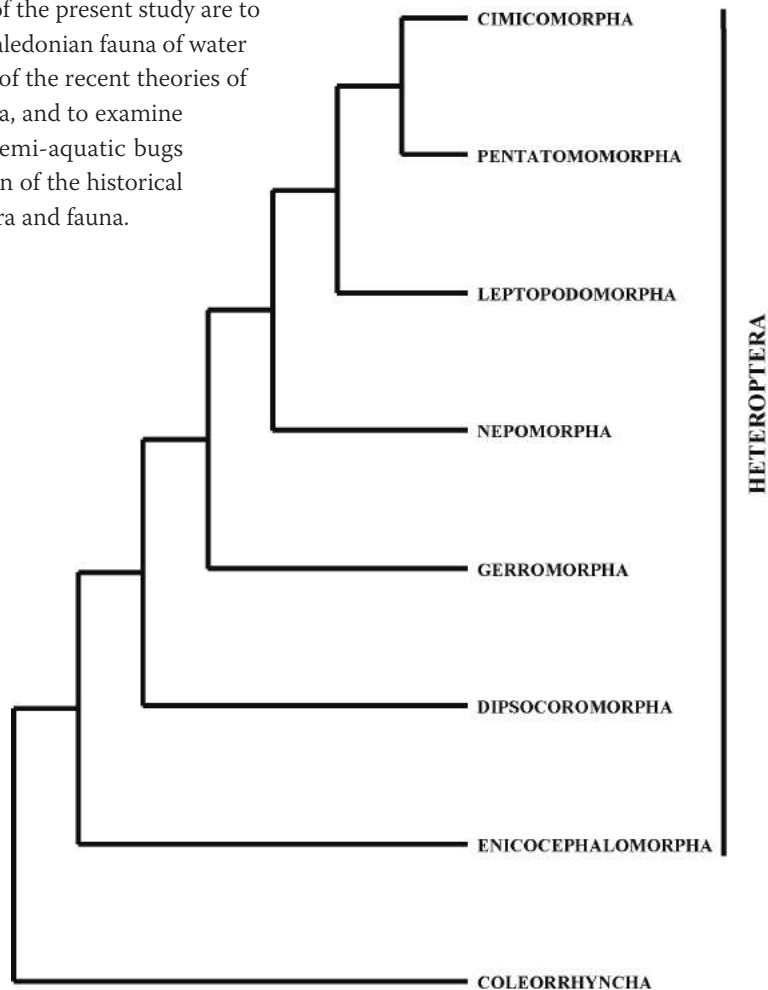


FIGURE 1

Phylogeny of heteropterans infra-orders according to Schuh & Slater (1995). All clades are present on New Caledonia.

THE NEW CALEDONIAN WATER-BUG FAUNA IN A WORLD PERSPECTIVE

Six of eight gerromorphan families are found in New Caledonia (Figure 2). The two families not present on New Caledonia are Macroveliidae that has three species described from the New World, and Paraphrynoveliidae, a group based on two species from South Africa (Andersen 1982; Schuh & Slater 1995). *Paraphrynovelia brinckii* (Poisson, 1956) was originally described as a relative of the mesoveliid *Phrynovelia papua* Horváth, 1915 from New Guinea but Andersen (1978) found it sufficiently distinct to erect a new family. Damgaard (2008a) showed that *Paraphrynovelia* and *Macrovelia* were so closely related that they probably belong to the same family, which means that only a single major clade of Gerromorpha is absent from New Caledonia.

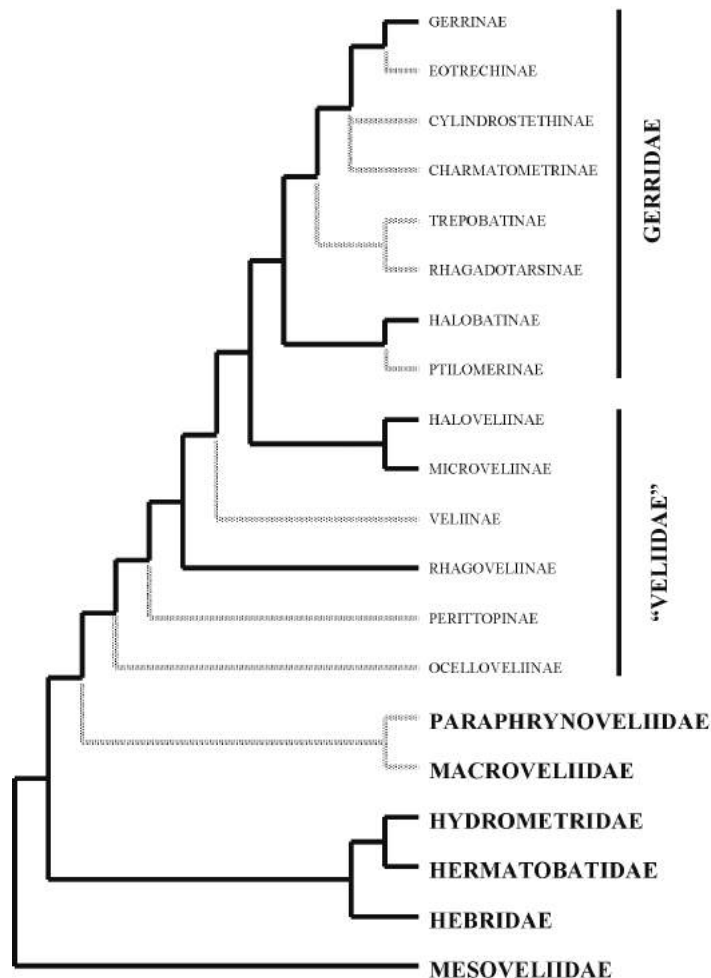
The largest two gerromorphan families, Veliidae and Gerridae, with more than 900 and 700 species respectively (Polhemus & Polhemus 2008a), are each represented in New Caledonia by only a few subfamilies, genera and species. Damgaard (2008a) found that the Gerridae were nested deeply within Veliidae and proposed that the Afro-tropical Ocelloveliinae be erected to a new family since the Gerridae plus remaining Veliidae were both clearly defined and had high branch support. How this would affect the Gerridae and the remaining subfamilies of Veliidae is dependent on future studies that must include both a higher taxon sample of genera and species and inspection of new molecular and morphological character systems.

Only five of thirteen subfamilies of the Veliidae + Gerridae clade are found in New Caledonia and all species belong to wide-spread genera. These are *Limnogonus* (“pond skaters”) (Gerridae: Gerrinae), *Halobates* (“sea skaters”) (Gerridae: Halobatinae), *Microvelia* (“pygmy water striders”) (Veliidae: Microveliinae), *Halovelia* (“coral bugs”) and *Xenobates* (“mangrove bugs”) (Veliidae: Haloveliinae) and *Rhagovelia* (“riffle bugs”) (Veliidae: Rhagoveliinae).

According to Damgaard *et al.* (2010), *Limnogonus* is primarily an Old World genus, but with two independent transitions to the New World. Members of *Limnogonus* are among the most frequently encountered water striders in the tropics, and the genus is predominantly represented in the Old World, but with two independent transitions to the New World (Damgaard *et al.* 2010). Andersen (1975: 25) showed that the Pacific islands offer some fascinating examples of ecological differentiation between species in that each of the larger islands indicates a similar pattern of community structure: one, two, or three recent immigrants and one endemic species. The pattern indicated by studies of the New Caledonia species could be seen as a noteworthy exception. *L. f. gilguy* and *L. luctuosus* are widespread in the region. However, Damgaard *et al.* (2010) showed that *L. luctuosus* from New Caledonia differs genetically and morphologically from conspecific material from the Society Is. (Moorea) and from Australia. Since the type locality for *L. luctuosus* is on New Caledonia, the other populations must be assigned to an yet undescribed species.

FIGURE 2

Phylogeny of Gerromorpha according to Damgaard (2008a). Taxa absent on New Caledonia are marked with faded branches.



Halobates, *Halovelina* and *Xenobates* are other Old World genera whose origin and primary diversities are in the tropical marine regions of the Indo-Pacific (Andersen 1982; Andersen & Cheng 2004; Chen *et al.* 2005). Several species are endemic to particular island groups, such as *Halobates panope* and *Xenobates loyaltiensis* from New Caledonia. Other species are more widespread. For example, *Halobates katherinae* is also recorded from nearby Vanuatu, 400–800 km north of Grande Terre (Nieser & Chen 2005) and *Halovelina hilli* is found also in Australia, New Guinea and East Timor (Andersen & Weir 2004a). Some marine species have truly extensive distributions in the Indo-Pacific Oceans - *Halovelina bergrothi*, *Halobates germanus* and *H. sericeus* (Andersen & Cheng 2004; Chen *et al.* 2005). Distant (1920) also listed *H. flaviventris* Eschscholtz, 1822 from New Caledonia, but the species was not recorded from this area by Andersen & Cheng (2004). Similarly, *Halobates flaviventris* was reported from Vanuatu by Herring (1961), but not by Nieser & Chen (2005). However, since the species is quite widespread, its occurrence in New Caledonia cannot be ruled out.

The large and cosmopolitan genus *Rhagovelia* has more than 300 described species, as well as many undescribed species (Polhemus & Polhemus 2008a), and includes some of the most commonly encountered semi-aquatic bugs on running waters in the tropics. Polhemus & Polhemus (1988) organised the Malesian *Rhagovelia* into several presumably monophyletic species groups and discussed their biogeographical relationships. From New Caledonia, they included *R. novacaledonica* and *R. pidaxa* and one undescribed species in the *R. novacaledonica*-group, which also included species from New Guinea and with other possible members in the Solomon Islands and the Philippines (see also Polhemus 1996). According to Polhemus & Polhemus (1988) the *R. novacaledonica*-group “is hypothesized to have originated on New Caledonia and to have subsequently dispersed northward along the intervening island arcs to New Guinea”.

Microveliinae is another large subfamily with more than 330 described species and many that are still awaiting formal description (Polhemus & Polhemus 2008a). Approximately half of the described species are assigned to the genus *Microvelia*, which includes quite uniform species, except for various modifications of the female abdomen and male genital segments, characters that are insufficiently known in many species (Andersen & Weir 2001). Both species from New Caledonia are assigned to the subgenus *Pacificovelia* Andersen & Weir 2003, which includes species from Japan, Australia, Papua New Guinea, Indonesia, New Zealand, Fiji, the Society Islands and the Hawaiian Islands and other surrounding areas (Andersen & Weir 2003).

The exclusively marine Hermatobatidae is one of the smallest of all gerromorphan families with ten extant species (Polhemus & Polhemus 2012). All species are assigned to *Hermatobates* and live in the Indo-Pacific Oceans, except for *H. breddini* Herring 1965 which is found in the Caribbean Sea (Herring 1965). Some species are widespread in coastal regions, e.g. *Hermatobates marcheii* which is found from Australia to the Ryukyu Islands in southern Japan, but others are endemic to small islands or island groups such as *H. armatus* from the Chesterfield Islands (Andersen & Weir 2000).

The Hydrometridae include approximately 125 species and is currently divided into three subfamilies: Hydrometrinae with five genera all over the World; Limnobatodinae with *Limnobatodes paradoxus* Hussey 1925 from tropical South America, and Heterocleptinae with *Velometra schuhi* Andersen 1977 from northern Brazil and four species of *Heterocleptes* from Africa and south-eastern Asia (Andersen 1982; Chen *et al.* 2005). Only members of the cosmopolitan *Hydrometra* are recorded from New Caledonia with one endemic species, *H. aculeata*, and one widespread species, *H. strigosa* (Andersen & Weir 2004a).

The Hebridae with more than 220 species (Polhemus & Polhemus 2008a) are currently divided into the Oriental Hyrcaninae with two genera, and the cosmopolitan Hebrinae with six genera. The single recorded species from New Caledonia still awaits formal description (Zettel & Damgaard in prep.), but belongs to the cosmopolitan genus *Hebrus*.

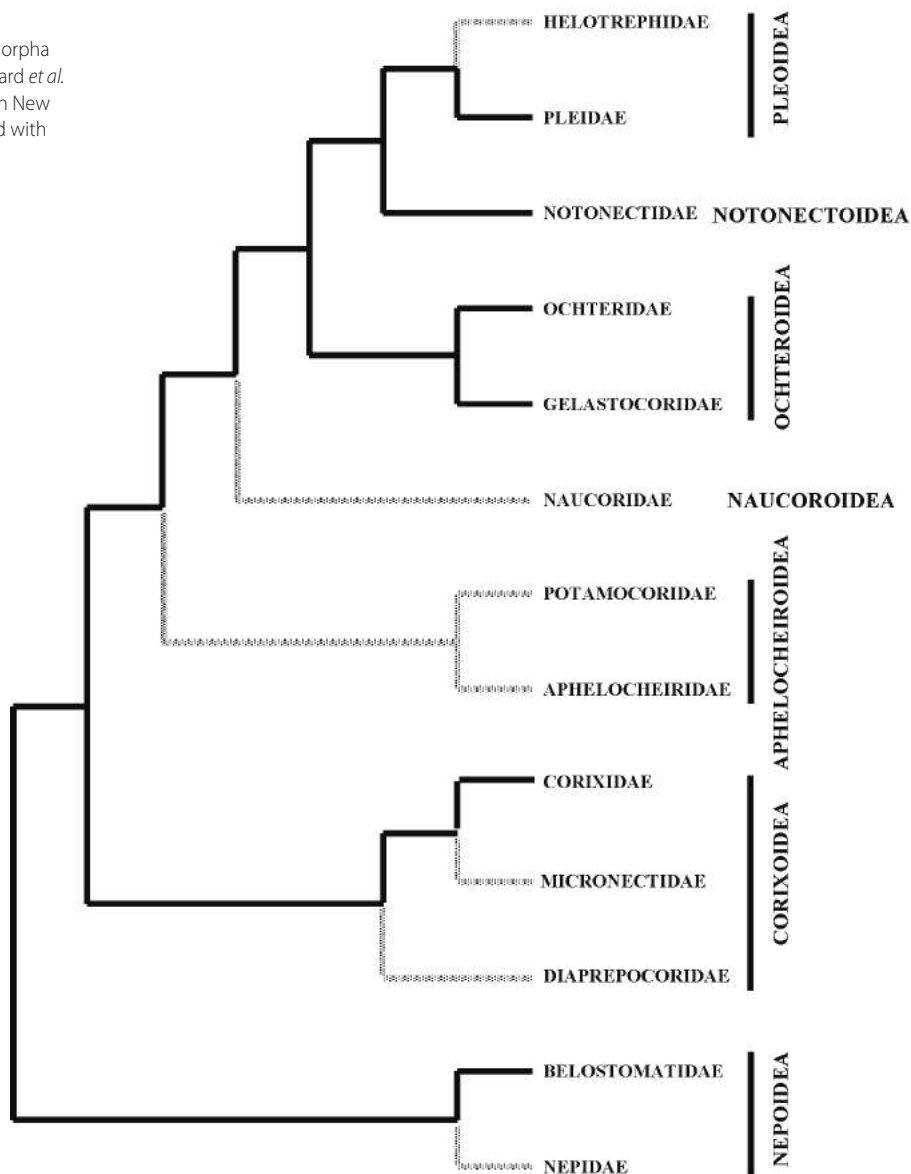
The family Mesoveliidae is sister group to all other families of Gerromorpha and is currently divided into two subfamilies, Madeoveliinae and Mesoveliinae (Andersen 1982). The Madeoveliinae contains *Madeovelia guineensis* Poisson, 1957 from Guinea in western Africa and *Mesoveloidea* Hungerford, 1929 with two species in the Neotropical Region. The Mesoveliinae contains 10 genera of which many are species-poor or even monotypic, but almost 30 species belong to the cosmopolitan genus *Mesovelia* (Damgaard *et al.* 2012). *Mesovelia* is represented in New Caledonia with *M. horvathi* and *M. vittigera* both of which have a wide distribution in the Australasian Region and beyond, and one endemic species still awaiting formal description (Zettel & Damgaard in prep.) Two other mesoveliine genera are represented by *Austrovelia caledonica*, *Phrynovelia bimaculata*, *P. caledonica* and an undescribed species of *Phrynovelia* (Zettel & Damgaard in

prep.). The single close relative of *Austrovelia caledonica* is *A. queenslandica* Malipatil & Monteith 1983 from mountain tops in northern Queensland, Australia (Andersen & Weir 2004a). *Phrynovelia* is represented by three endemic species, *P. bimaculata*, *P. caledonica*, and one species awaiting formal description (Zettel & Damgaard in prep.). Besides the aforementioned *P. papua*, the only other species assigned to *Phrynovelia* is the somehow aberrant *P. philippinensis* Zettel, 2004 from Polillo Island near Luzon in the Philippines (Zettel 2004). Andersen & Polhemus (1980) mentioned a possible species from cloud forests on the Seychelles in the Indian Ocean, but despite many phenotypic similarities, this species was later assigned to a new, monotypic genus, *Seychellovelia* Andersen & Polhemus, 2003 (Andersen & Polhemus 2003).

Six of 13 nepomorphan families are listed from New Caledonia (Figure 3), one of which, Gelastocoridae, was recorded only recently (Cassis & Silveira 2006). Among the families not represented in the New Caledonian fauna, the Potamocoridae have a strict Neotropical distribution (Schuh & Slater 1995) and cannot be expected in New Caledonia,

FIGURE 3

Phylogeny of Nepomorpha according to Hebsgaard *et al.* (2004). Taxa absent on New Caledonia are marked with faded branches.



while Helotrephidae, despite having a circumtropical distribution, have not been found in Malesia east of Sulawesi (Chen *et al.* 2005). The families Nepidae, Micronectidae, Naucoridae and Aphelocheiridae are widespread in Malesia, and occur in Australia (Andersen & Weir 2004a; Tinerella 2008), while Diaprepocoridae, considered to be sister group to all other Corixoidea, have a Bassian distribution with three species in southern Australia (including Tasmania) and a single species in New Zealand (Andersen & Weir 2004a).

The Belostomatidae with approximately 160 species are divided into three subfamilies: Horvathiniinae from the Neotropical Region and Belostomatinae and Lethocerinae which are found in all the world's tropical and subtropical zones (Schuh & Slater 1995; Polhemus & Polhemus 2008a). Only the circumtropical genus *Lethocerus* is present in New Caledonia.

The Corixidae currently include the large cosmopolitan Corixinae with hundreds of species worldwide and the small subfamilies Cymatiinae (with *Cymatia* in the Holarctic and *Cnetocymatia* from northern Australia and New Guinea), Heterocorixinae (with *Heterocorixa* in the Neotropical Region) and Stenocorixinae with *Stenocorixa protrusa* Horváth from Africa). All New Caledonian species can be assigned to the circumtropical subgenus *Sigara* (*Tropocorixa*), except *Trichocorixa verticalis verticalis* (Fieber, 1851), which was probably introduced and released along with mosquito fish from eastern North America during Second World War, when an American army base was established on the island (Jansson 1982).

The Ochteridae currently include *Megochterus* with two species in Australia (Andersen & Weir 2004a) and the cosmopolitan *Ochterus* with approximately 70 species (Polhemus & Polhemus 2008a) of which *Ochterus dufourii* is endemic to New Caledonia. Like the Ochteridae, the Gelastocoridae are terrestrial, and comprise approximately 110 species (Polhemus & Polhemus 2008a) in the New World genus *Gelastocoris* and the circumtropical *Nerthra*, which has radiated extensively in Australia (Andersen & Weir 2004a).

The Pleidae contain almost 40 species of tiny aquatic bugs (Polhemus & Polhemus 2008a), and the genus *Paraplea* is widespread in the Malesian Region (Chen *et al.* 2005). Finally, the Notonectidae with approximately 400 species (Polhemus & Polhemus 2008a) are subdivided into the Anisopinae and the Notonectinae, both of which include many genera throughout the world. Both genera present in New Caledonia, *Anisops* and *Enithares*, are wide spread in the Old World.

ORIGIN AND DIVERSITY OF THE NEW CALEDONIAN WATER BUG FAUNA

Compared to the endemism of other arthropods of a high taxonomic rank, the absence of endemic genera of water bugs on New Caledonia is striking, especially when compared to the high number in neighboring areas such as Australia (Andersen & Weir 2004a) and New Guinea (Chen *et al.* 2005). Other islands in the vicinity of New Caledonia also have their own endemic genera - New Zealand (*Mniovelina* Andersen & Polhemus, 1980), Fiji (*Fijivelina* Polhemus & Polhemus, 2006) and even tiny islands such as Tubuai (*Tubuaivelina* Polhemus & Polhemus, 2008b) and Lord Howe Island (*Nesidovelina* Andersen & Weir, 2001) (Andersen & Polhemus 1980; Andersen & Weir 2001; Polhemus & Polhemus 2006; 2008b). While in *Microvelia* every specially adapted clade has been described as its own genus, leading to a wealth of new subgeneric taxa, in *Rhagovelina* even subgenera were abandoned and there are only informal species groups which, like the *R. novacaledonica* group, might be of similar significance (or age), *e.g.*, *Fijivelina*. At the species level, the majority of New Caledonian water bugs are either endemic to New Caledonia and associated islands (17 species) or shared with surrounding landmasses and islands, in particular Australia (Andersen & Weir 2004a), New Guinea (Chen *et al.* 2005), and Vanuatu (Nieser & Chen 2005), but also New Zealand (Larivière & Laroche 2004), Norfolk Island (Andersen & Weir 2004a), Lord Howe Island (Andersen & Weir 2004a; Buzzetti *et al.* 2006) and beyond (Table 1). Many water bugs are known for excellent dispersal abilities, and even though only species with macropterous individuals are capable of flight, hurricanes are considered to have played role in the long-distance dispersal of gerromorphan bugs (Herring 1958a). *Mesovelina vittigera* is one of the most widely distributed species, occurring in the subtropical regions of the Palearctic Region, the entire Afrotropical, Oriental, Malesian and Australian Regions, and far-flung islands of the western Pacific Ocean (Andersen & Weir 2004a). Other widely distributed species include *Mesovelina horvathi*, *Hydrometra strigosa*, *Microvelia* (*Pacificovelina*) *oceanica*, *Limnogonus fossarum gilguy*, *Lethocerus insulani*, *Ochterus australicus*, *Sigara* (*Tropocorixa*)

tadeuszi, *S. (T.) truncatipala*, *Paraplea liturata*, *Anisops cleopatra*, *A. crinitus*, *A. hyperion*, and *A. occipitalis*. Until the underlying genetic structure is known, it is reasonable to assume that wide-spread species from New Caledonia are part of much larger and more-or-less panmictic populations maintained through occasional dispersal by air or perhaps by unintended re-introductions. The presence of numerous marine gerromorphans on New Caledonia is also expected, since the western Pacific is a “hot spot” area for diversification of this group (Andersen & Weir 2004a). Even though most species are confined to coastal environments, it is possible that some individuals occasionally may cross large stretches of water, perhaps mediated by violent storms. In total, nine of 25 species, corresponding to 36% of the New Caledonian fauna of Gerromorpha are confined to marine environments, which is much more so than in Australia (24%) and far in excess of the world average (10%) (Andersen & Weir 2004a). The higher percentage of endemic species of Gerromorpha (52%) as compared to Nepomorpha (31%) is an interesting feature, since both groups seem equally capable of dispersal. What is more peculiar is that two of three endemic nepomorphan species are terrestrial, which lowers the number of endemic truly aquatic bugs to *Enithares bergrothi*.

Peloriidiids, enicocephalids, dipsocorids, gelastocorids, ochterids, and many gerromorphan lineages live in moist terrestrial habitats. This feature is likely to represent the ancestral lifestyle of all Heteroptera (Andersen 1982). From this type of habitat, the Nepomorpha evolved to an entirely aquatic lifestyle, with a secondary reversal to the terrestrial environment in the common ancestor of Ochteridae and Gelastocoridae (Hebsgaard *et al.* 2004). In Gerromorpha, adaptation to a life on the surface of water has probably evolved several times independently, just as the transition from limnic to marine habitats and from coastal to open-ocean environments: and some lineages have even returned to the terrestrial environment (Andersen 1982; Spence & Andersen 1994; Damgaard *et al.* 2000). Mesoveliidae is a well-established sister

TABLE 1

Overlapping distributions of New Caledonian water bugs with neighboring land masses in the south-western Pacific Ocean. AUS (continental Australia), NG (New Guinea), VAN (Vanuatu), SI (Solomon Is.), FIJ (Fiji), LHI (Lord Howe Island), NFI (Norfolk Island), NZ (New Zealand).

LAND MASS	AUS	NG	VAN	SI	FIJ	LHI	NFI	NZ
<i>Mesovelia horvathi</i>	X	X	-	-	-	-	-	-
<i>Mesovelia vittigera</i>	X	X	X	-	-	-	-	-
<i>Hydrometra strigosa</i>	X	-	X	X	-	X	X	X
<i>Hermatobates marcheii</i>	-	X	-	-	-	X	-	-
<i>Halovelia bergrothi</i>	-	X	-	X	-	-	-	-
<i>Halovelia hilli</i>	X	X	-	-	-	-	-	-
<i>Microvelia oceanica</i>	X	-	X	-	X	X	X	-
<i>Limnogonus fossarum gilguy</i>	X	X	X	X	X	-	-	-
<i>Halobates germanus</i>	X	X	X	X	X	-	-	-
<i>Halobates katherinae</i>	-	-	X	-	-	-	-	-
<i>Halobates sericeus</i>	X	-	-	-	X	X	-	X
<i>Lethocerus insulanus</i>	X	X	-	-	-	-	-	-
<i>Ochterus australicus</i>	X	-	X	X	-	-	-	-
<i>Sigara truncatipala</i>	X	X	X	-	-	X	-	-
<i>Paraplea liturata</i>	X	X	X	-	-	-	-	-
<i>Anisops hyperion</i>	X	-	-	-	-	-	-	-
<i>Anisops occipitalis</i>	X	X	-	X	-	-	-	-
no. identical species	15	10	9	6	5	4	2	2

group to all other gerromorphan families (Damgaard 2008a), and Andersen (1982) considered the occurrence of the many island-endemic and monotypic or species-poor genera to be due to “primitive cosmopolitanism”, i.e. the result of relictual lineages in isolated areas without competition from more derived forms. The many terrestrial species of Mesoveliidae could lead to speculation that these represent the ancestral habitat preferences of the family, but the few phylogenetic studies so far have resulted in little support for this idea (Andersen & Polhemus 1980; Andersen 1999). However, due to the antiquity of the group and many likely instances of convergent evolution, most of all by the reduction of external features as an adaptation to life in cryptic terrestrial habitats, not much emphasis may be put on these phylogenetic reconstructions, and it is highly desirable that the phylogenetic relationships of Mesoveliidae be re-considered on the basis of new molecular evidence.

New Caledonia may be seen as a “hot spot” for the diversification of Mesoveliidae as the islands are home to more than 15% of the world fauna (Damgaard *et al.* 2012). Seven species (five endemic) in three genera is comparable to that of all Australia with seven species (two endemic) in two genera (Andersen & Weir 2004a, b) and all of Malesia with nine species (several endemic to particular islands) in four genera (Chen *et al.* 2005). The most interesting feature of the fauna is the presence of at least half the known species of *Austrovelia* and *Phrynovelia*. These two groups of wingless terrestrial gerromorphans inhabit the same environment as the peloridiids and enicocephalids and, like these, probably date back to the time before the splitting up of Gondwana. That such tiny, fragile and flightless insects can cross hundreds of kilometers of open, tropical waters seems highly unlikely.

Despite growing biogeographical evidence that New Caledonia is an old Darwinian island and not an ark for Gondwanan relicts—even for some groups that are restricted to land areas that used to be parts of Gondwana (Heads 2008)—and also that much of its flora and fauna are newcomers (Murienne *et al.* 2005, 2008; Grandcolas *et al.* 2008), there are other studies suggesting that at least some parts of the biota may have a much older origin (Ladiges & Cantrill 2007). Studies of the largely unexplored, but highly diverse, fauna of terrestrial invertebrates may reveal different biogeographical patterns, which again may necessitate different explanations, such as has also been suggested for nearby New Zealand (Gibbs 2006).

There is no doubt that all families and probably most subfamilies of water bugs were present long before the break-up of Gondwanaland, and that the distribution of mesoveliid genera, especially the many island endemics, probably represents a type of “primitive cosmopolitanism” (Andersen 1982; Andersen & Polhemus 2003). However, the absence of many families, subfamilies and genera found in Australia and New Guinea is an equally good argument for an alternative view. For instance, the Diaprepocoridae have been recorded from the Upper Jurassic of Europe and Central Asia (Popov 1971), and considering the many other phylogenetic relicts, one would have expected this taxon to be present in New Caledonia.

Recent evidence has suggested that extant genera are also of considerable age (Andersen 1998; Garrouste & Nel 2010) and the logical next step in investigating the New Caledonian water bug fauna will be to reconstruct phylogenies of species assigned to more widespread genera and species groups. When summarizing the biogeography of the *Rhagovelia novacaledonica* group Polhemus & Polhemus (1988) considered the area as “a generally overlooked reservoir of tropical Gondwanaland taxa that have contributed southern elements to the present biota of New Guinea”. Such a view may also include other clades, such as *Mesovelia*, *Hebrus*, *Hydrometra*, *Microvelia* (*Pacificovelia*), *Enithares*, *Nerthra*, *Ochterus*, and *Sigara* (*Tropocorixa*), but confirmation will require the construction of more robust species phylogenies.

ACKNOWLEDGMENTS

The authors wish to thank the following persons for contributing material for this study: Michael Balke, Geoff Monteith and Christian Millet. The Villum Kann Rasmussen Foundation is thanked for its continuous support of the senior author's work on water bugs and for supporting his visit to New Caledonia in 2008.

REFERENCES

- ANDERSEN N.M. 1975 — The *Limnogonus* and *Neogerris* of the Old World with character analysis and a reclassification of the Gerrinae (Hemiptera: Gerridae). *Entomologica Scandinavica*, Supplementum 7: 1-96.
- ANDERSEN N.M. 1978 — A new family of semiaquatic bugs for *Paraphrynovelia* Poisson with a cladistic analysis of relationships (Insecta, Hemiptera, Gerromorpha). *Steenstrupia* 19 (4): 211-225.
- ANDERSEN N.M. 1982 — *The semiaquatic bugs (Hemiptera, Gerromorpha). Phylogeny, adaptations, biogeography, and classification*. Scandinavian Science Press, Klampenborg (Denmark), 455 p. (Entomonograph; 3)
- ANDERSEN N.M. 1989 — The coral bugs, genus *Halovelia* Bergroth (Hemiptera, Veliidae). 1. History, classification, and taxonomy of species except the *H. malaya*-group. *Entomologica Scandinavica* 20: 75-120.
- ANDERSEN N.M. 1998 — Water striders from the Palaeocene of Denmark with a review of the fossil record and evolution of semiaquatic bugs (Hemiptera: Gerromorpha). *Det Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter* 50: 1-152.
- ANDERSEN N.M. 1999 — *Cryptovelia stysi* sp. n. from Borneo with a reanalysis of the phylogeny of the Mesoveliidae (Heteroptera: Gerromorpha). *Acta Societatis Zoologicae Bohemicae* 63: 5-18.
- ANDERSEN N.M. & CHENG L. 2004 — The marine insect *Halobates* (Heteroptera: Gerridae): Biology, adaptations, distribution and phylogeny. *Oceanography and Marine Biology: An Annual Review* 42: 119-180.
- ANDERSEN N.M. & POLHEMUS D.A. 2003 — A new genus of terrestrial Mesoveliidae from the Seychelles (Hemiptera: Gerromorpha). *Journal of the New York Entomological Society* 111(2): 12-21.
- ANDERSEN N.M. & POLHEMUS J.T. 1980 — Four new genera of Mesoveliidae (Hemiptera, Gerromorpha) and the phylogeny and classification of the family. *Entomologica Scandinavica* 11: 369-392.
- ANDERSEN N.M. & WEIR T.A. 1997 — The gerrine water striders of Australia (Hemiptera: Gerridae): taxonomy, distribution, and ecology. *Invertebrate Taxonomy* 11: 203-299.
- ANDERSEN N.M. & WEIR T.A. 1999 — The marine Haloveliinae (Hemiptera: Veliidae) of Australia, New Caledonia, and southern New Guinea. *Invertebrate Taxonomy* 13: 309-350.
- ANDERSEN N.M. & WEIR T.A. 2000 — The coral treaders, *Hermatobates* Carpenter (Hemiptera, Hermatobatidae), of Australia and New Caledonia, with notes on biology and ecology. *Invertebrate Taxonomy* 14: 327-345.
- ANDERSEN N.M. & WEIR T.A. 2001 — New genera of Veliidae (Hemiptera-Heteroptera) from Australia, with notes on the generic classification of the Microveliinae. *Invertebrate Taxonomy* 15: 217-258.
- ANDERSEN N.M. & WEIR T.A. 2003 — The genus *Microvelia* Westwood in Australia (Hemiptera: Heteroptera: Veliidae). *Invertebrate Systematics* 17: 261-348.
- ANDERSEN N.M. & WEIR T.A. 2004a — *Australian water bugs (Hemiptera-Heteroptera, Gerromorpha & Nepomorpha) their biology and identification*. Apollo Books, Stenstrup (Denmark); CSIRO Pub, Collingwood (VIC, Australia), 344 p. (Entomonograph; 15).
- ANDERSEN N.M. & WEIR T.A. 2004b — Mesoveliidae, Hebridae, and Hydrometridae of Australia (Hemiptera: Heteroptera: Gerromorpha), with a reanalysis of the phylogeny of semiaquatic bugs. *Invertebrate Systematics* 18: 467-522.
- AUKEMA B. & RIEGER C. 1995 — *Catalogue of Palaearctic Heteroptera 1. Enicocephalomorpha, Dipsocoromorpha, Nepomorpha, Gerromorpha and Leptopodomorpha*. The Netherlands Entomological Society, Amsterdam, 222 p.
- BAEHR M. 1989 — Revision of the genus *Ochterus* Latreille in the Australian region (Heteroptera: Ochteridae). *Entomologica Scandinavica* 20: 449-477.
- BALKE M., WEWALKA G., ALARIE Y. & RIBERA I. 2007a — Molecular phylogeny of Pacific Island Colymbetinae: radiation of New Caledonian and Fijian species (Coleoptera, Dytiscidae). *Zoologica Scripta* 36: 173-200.
- BALKE M., PONS J., RIBERA I., SAGATA K. & VOGLER A.P. 2007b — Infrequent and unidirectional colonization of hyperdiverse *Papuadytes* diving beetles in New Caledonia and New Guinea. *Molecular Phylogenetics and Evolution* 42: 505-516.
- BREDDIN G. 1905 — Rhynchota Heteroptera aus Java, gesammelt von Prof. K. Kraepelin 1904. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg* 22: 110-159.
- BROOKS G.T. 1951 — A revision of the genus *Anisops* (Notonectidae, Hemiptera). *University of Kansas Scientific Bulletin* 24: 301-519.
- BURCKHARDT D. 2009 — Taxonomy and phylogeny of the Gondwanan moss bugs or Peloridiidae (Hemiptera, Coleorrhyncha). *Deutsche Entomologische Zeitschrift* 56 (2): 173-235.
- BUZZETTI F.M., NIESER N. & DAMGAARD J. 2006 — Notes on water bugs from South East Asia and Australia. *Atti dell'Accademia Roveretana degli Agiati, Contributi della Classe di Scienze Matematiche, Fisiche e Naturali* ser. VIII, B, 256: 31-45.
- CASSIS G., SCHWARTZ M.D. & MOULDS T. 2003 — Systematics and new taxa of the Vannius complex (Hemiptera: Miridae: Cylapinae) from the Australian Region. *Memoirs of Queensland Museum* 49: 125-143.
- CASSIS G. & SILVEIRA R. 2006 — A new species and first record of a toad bug (Insecta: Heteroptera: Gelastocoridae) from New Caledonia and zoogeography. *Russian Entomological Journal* 15 (2): 141-146.
- CHEN P.-P., NIESER N. & ZETTEL H. 2005 — The aquatic and semi-aquatic bugs (Heteroptera: Nepomorpha & Gerromorpha) of Malesia. *Fauna Malesiana Handbook* 5: 1-546.
- CHINA W.E. 1957 — The marine Hemiptera of the Monte Bello Islands, with descriptions of some allied species. *Zoological Journal of the Linnaean Society* 40: 342-357.
- DAMGAARD J. 2008a — Phylogeny of the semiaquatic bugs (Hemiptera-Heteroptera, Gerromorpha). *Insect Systematics and Evolution* 39: 431-460.
- DAMGAARD J. 2008b — Evolution of the semi-aquatic bugs (Hemiptera: Heteroptera: Gerromorpha) with a re-interpretation of the fossil record. *Acta Entomologica Musei Nationalis Pragae* 48(2): 251-268.
- DAMGAARD J., ANDERSEN N.M., CHENG L. & SPERLING F.A.H. 2000 — Phylogeny of sea skaters, *Halobates* Eschscholtz (Hemiptera, Gerridae), based on mtDNA sequence and morphology. *Zoological Journal of the Linnaean Society* 130(4): 511-526.
- DAMGAARD J., BUZZETTI F.M., MAZZUCCONI S.A., WEIR T.A. & ZETTEL H. 2010 — A molecular phylogeny of the pan-tropical pond skater genus *Limnogonus* Stål 1868 (Hemiptera-Heteroptera: Gerromorpha-Gerridae). *Molecular Phylogenetics and Evolution* 57: 669-677.
- DAMGAARD J., MOREIRA F.F.F., HAYASHI M., WEIR T.A. & ZETTEL H. 2012 — Molecular phylogeny of the pond treaders (Insecta: Hemiptera: Heteroptera: Mesoveliidae), discussion of the fossil record and a checklist of species assigned to the family. *Insect Systematics and Evolution* 43: 175-212.

- DISTANT W. L. 1914 — Rhynchota from New Caledonia and the surrounding islands, in SARASIN F. & ROUX J. (eds), *Nova Caledonia, A. Zoologie*, vol. 1 (4), C.W. Kreidels Verlag, Wiesbaden: 369-391, pls. 11-12.
- DISTANT W. L. 1920 — Rhynchota from New Caledonia. *Annual Magazine of Natural History* 9 (6): 143-164.
- DREW B. T., RUHFEL B. R., SMITH S. A., MOORE M. J., BRIGGS B. G., GITZENDANNER M. A., SOLTIS P. S. & SOLTIS D. E. 2014 — Another Look at the root of the Angiosperms reveals a familiar tale. *Systematic Biology* 63 (3): 368-382.
- EDGEcombe G. D. & GIRIBET G. 2009 — Phylogenetics of scutigeromorph centipedes (Myriapoda: Chilopoda) with implications for species delimitation and historical biogeography of the Australian and New Caledonian faunas. *Cladistics* 25: 406-427.
- ESAKI T. 1926 — The water-striders of the subfamily Halobatinae in the Hungarian National Museum. *Annales Musei Nationalis Hungarici* 23: 117-164.
- ESCHSCHOLTZ J. F. 1822 — *Entomographien, vol. 1 (Erste Lieferung)*, Reimer, Berlin, 128 p.
- EVANS J. W. 1981 — A review of present knowledge of the family Peloriidae and new genera and new species from New Zealand and New Caledonia (Hemiptera: Insecta). *Records of the Australian Museum* 34(5): 381-406.
- FIEBER F. X. 1851 — Species generis *Corisa* monographice dispositae. *Abhandlungen der Königlichen Böhmischen Gesellschaft der Wissenschaften* (5) 7: 213-260, tab. I-II.
- GARROUSTE R. & NEL A. 2010 — First semi-aquatic bugs Mesoveliidae and Hebridae (Hemiptera: Heteroptera: Gerromorpha) in Miocene Dominican amber. *Insect Systematics & Evolution* 41(2): 93-102.
- GIBBS G. 2006 — *Ghosts of Gondwana. The History of Life in New Zealand*. Craig Potton Publishing, Nelson, N. Z., 234 p.
- GRANDCOLAS P., MURIENNE J., ROBILARD T., DESUTTER-GRANDCOLAS L., JOURDAN H. & GUILBERT É. 2008 — New Caledonia: a very old Darwinian island? *Philosophical Transactions from the Royal Society of London series B Biological Sciences* 363: 3309-3317.
- HACKETT S. J., KIMBALL R. T., REDDY S., BOWIE R. C. K., BRAUN E. L., CHOJNOWSKI J. L., COX W. A., HAN K.-L., HARSHMAN J., HUDDLESTON C. J., MARKS B. D., MIGLIA K. J., MOORE W. S., SHELTON F. H., STEADMAN D. W., WITT C. C. & YURI T. 2008 — A phylogenomic study of birds reveals their evolutionary history. *Science* 320 (5884): 1763-1768.
- HALE H. M. 1922 — Studies in Australian aquatic Hemiptera No. 1. *Records of the South Australian Museum* 2: 309-330.
- HEADS M. 2008 — Panbiogeography of New Caledonia, south-west Pacific: basal angiosperms on basement terranes, ultramafic endemics inherited from volcanic island arcs and old taxa endemic to young islands. *Journal of Biogeography* 35: 2153-2175.
- HEBSGAARD M. B., ANDERSEN N. M. & DAMGAARD J. 2004 — Phylogeny of the true water bugs (Nepomorpha: Hemiptera-Heteroptera) based on 16S and 28S rDNA and morphology. *Systematic Entomology* 29: 488-508.
- HENRY T. J. & FROESCHNER R. C. (eds) 1988 — *Catalog of the Heteroptera or True Bugs of Canada and the Continental United States*. E. J. Brill, New York, 958 p.
- HERRING J. L. 1958a — Evidence for hurricane transport and dispersal of aquatic Hemiptera. *Pan Pacific Entomologist* 34: 174-175.
- HERRING J. L. 1958b — The marine water-striders of the "Dana" Expeditions (Insecta: Hemiptera). *Dana report* 44: 1-14.
- HERRING J. L. 1961 — The genus *Halobates* (Hemiptera: Gerridae). *Pacific Insects* 3: 223-305.
- HERRING J. 1965 — *Hermatobates*, a new generic record for the Atlantic Ocean, with descriptions of new species (Hemiptera: Gerridae). *Proceedings of the U.S. National Museum* 117: 123-130.
- HORVÁTH G. 1895 — Hémiptères nouveaux d'Europe et des pays limitrophes. *Revue d'Entomologie* 14 (5 + 6-7): 152-165.
- HUNGERFORD H. B. 1938 — A new Hydrometra from New Caledonia and Australia. *Pan-Pacific Entomologist* 14: 81-83.
- JACZEWSKI T. 1934 — Notes on the Old World species of Ochteridae (Heteroptera). *Annals and Magazine of Natural History* (10) 11: 597-613.
- JÄCH M. A. & BALKE M. 2010 — Water Beetles of New Caledonia, volume 1. *Monographs on Coleoptera* 3: 323-364.
- JANSSON A. 1982 — Notes on some Corixidae (Heteroptera) from New Guinea and New Caledonia. *Pacific Insects* 24 (1): 95-103.
- JANSSON A. & REAVELL P. E. 1999 — North American species of Trichocorixa (Heteroptera: Corixidae) introduced into Africa. *African Entomology* 7 (2): 295-297.
- KIRKALDY G. W. 1898 — Neue und seltene Notonectiden-Arten. *Wiener Entomologische Zeitung* 17: 141-142.
- LADIGES P. Y. & CANTRILL D. 2007 — New Caledonia-Australian connections: biogeographic patterns and geology. *Australian Journal of Systematic Botany* 20: 383-389.
- LANSBURY I. 1968 — The Enithares (Hemiptera: Heteroptera: Notonectidae) of the Oriental Region. *Pacific Insects* 10 (2): 353-442.
- LANSBURY I. 1970 — Revision of the Australian *Sigara* (Hemiptera-Heteroptera, Corixidae). *Journal of Natural History* 4 (1): 39-54.
- LARIVIÈRE M.-C. & LAROCHELLE A. 2004 — Heteroptera (Insecta: Hemiptera): catalogue. *Fauna of New Zealand* 50: 330 p.
- LUNDBLAD O. 1933 — Zur Kenntnis der aquatilen und semi-aquatilen Hemipteren von Sumatra, Java und Bali auf Grund des Materials der Deutschen Limnologischen Sunda-Expedition, nebst Revision einiger anderer, indoaustralischer Arten. *Archiv für Hydrobiologie, Supplementband* 12 (Tropische Binnengewässer IV): 1-195 / 263-489, 21 pls.
- LUNDBLAD O. 1936 — Die altweltlichen Arten der Veliidengattungen Rhagovelia und Tetraripis. *Arkiv för Zoologi* 28A(21): 1-63, 13 pls.
- MALIPATIL M. B. & MONTEITH G. B. 1983 — One new genus and four new species of terrestrial Mesoveliidae (Hemiptera: Gerromorpha) from Australia and New Caledonia. *Australian Journal of Zoology* 31: 943-955.
- MCLOUGHLIN S. 2001 — The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany* 49: 271-300.
- MONTANDON A. 1892 — Deux hémiptères nouveaux (section des Hydrocorises Latr.). *Revue d'Entomologie* 11: 73-76.
- MONTANDON A. 1898 — Hemiptera Cryptocerata. Notes et descriptions d'espèces nouvelles. *Bulletin de la Société Bucarest* 7: 430-432.
- MONTROUZIER P. 1864 — Essai sur la faune entomologique de Kanala (Nouvelle-Calédonie) et description de quelques espèces nouvelles ou peu connues. *Annales de la Société Linnéenne de Lyon*. Nouvelle 11: 46-256, 1 pl.
- MURIENNE J. 2009 — Testing biodiversity hypotheses in New Caledonia using phylogenetics. *Journal of Biogeography* 36: 1433-1434.
- MURIENNE J., GRANDCOLAS P., PIULACHS M. D., BELLÉS Z., D'HAESE C. A., PELLENS R. & GUILBERT É. 2005 — Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? *Cladistics* 21: 2-7.
- MURIENNE J., PELLENS R., BUDINOFF R. B., WHEELER W. C. & GRANDCOLAS P. 2008 — Phylogenetic analysis of the endemic New Caledonian cockroach

- Lauraesilpha*. Testing competing hypotheses of diversification. *Cladistics* 24: 1-11.
- NIESER N. & CHEN P.-P. 2005 — The water bugs (Hemiptera: *Nepomorpha* and *Gerromorpha*) of Vanuatu. *Tijdschrift voor Entomologie* 148: 307-327.
- OUVRARD D., CAMPBELL B. C., BOURGOIN T. & CHAN K. L. 2000 — 18S rRNA secondary structure and phylogenetic position of Peloridiidae (Insecta, Hemiptera). *Molecular Phylogenetics and Evolution* 16(3): 403-417.
- PELLETIER B. 2006 — Geology of the New Caledonia region and its implications for the study of the New Caledonian biodiversity, in PAYRI C. E. & RICHER DE FORGES B. (eds), *Compendium of marine species from New Caledonia*. IRD, Nouméa, New Caledonia: 19-32 (Dossiers Scientifiques et Techniques, II).
- POISSON R. 1957 — Chapter 8, Hemiptera Heteroptera: Hydrocorisae & Geocorisae-Gerroidea. *South African Animal Life* 4: 327-373.
- POLHEMUS D. A. 1996 — Two new species of *Rhagovelia* from the Philippines, with a discussion of zoogeographic relationships between the Philippines and New Guinea (Heteroptera: Veliidae). *Journal of the New York Entomological Society* 103(1): 55-68.
- POLHEMUS J. T. & HERRING J. L. 1970a — Ergebnisse der Österreichischen Neukaledonien Expedition. Aquatic and semiaquatic Hemiptera. *Proceedings of the Entomological Society of Washington* 72(2): 179-187.
- POLHEMUS J. T. & HERRING J. L. 1970b — Études hydrobiologiques en Nouvelle Calédonie (Mission 1965 du Premier Institute de Zoologie de L'Université de Vienne (Suite)* X. Aquatic and Semi-aquatic Hemiptera of New Caledonia. *Cahiers ORSTOM, Série Hydrobiologique* 4(2): 3-12.
- POLHEMUS J. T. & LANSBURY I. 1997 — Revision of the genus *Hydrometra* Latreille in Australia, Melanesia, and the Southwest Pacific (Heteroptera: Hydrometridae). *Bishop Museum Occasional Papers* 47: 1-67.
- POLHEMUS J. T. & POLHEMUS D. A. 1988 — Zoogeography, ecology, and systematics of the genus *Rhagovelia* Mayr (Heteroptera: Veliidae) in Borneo, Celebes, and the Moluccas. *Insecta Mundi* 2(3-4): 161-230.
- POLHEMUS J. T. & POLHEMUS D. A. 2001 [2000] — The genus *Mesovelia* Mulsant & Rey in New Guinea (Heteroptera: Mesoveliidae). *Journal of the New York Entomological Society* 108(3-4): 205-230.
- POLHEMUS J. T. & POLHEMUS D. A. 2006 — A new genus and two new species of Microveliinae from Fiji (Heteroptera: Veliidae). *Russian Journal of Entomology* 15(2): 181-186.
- POLHEMUS J. T. & POLHEMUS D. A. 2008a — Global diversity of true bugs (Heteroptera; Insecta) in freshwater. *Hydrobiologia* 595(1): 379-391.
- POLHEMUS J. T. & POLHEMUS D. A. 2008b — A new genus of Microveliinae from Austral Islands, French Polynesia (Heteroptera, Veliidae), in GROZEVA S. & SIMOV N. (eds), *Advances in Heteroptera Research. Festschrift in Honour of 80th Anniversary of Michail Josifov*. Pensoft Publishers, Sofia; Moscow: 293-302.
- POLHEMUS J. T. & POLHEMUS D. A. 2012 — A review of the genus *Hermatobates* (Heteroptera: Hermatobatidae), with descriptions of two new species. *Entomologica Americana* 118(1): 20-241.
- POPOV Y. A. 1971 — The historical development of Hemiptera infraorder Nepomorpha (Heteroptera). *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 129: 1-230 (in Russian; informal translation in English by Miss. H. Vaitaitis; 1-141; Arlington, USA).
- POPOV Y. A. & BECHLY G. 2007 — Heteroptera: Bugs, in MARTILL D. M., BECHLY G. & LOVERIDGE R. F. (eds), *The Crato Fossil Beds of Brazil. Window to an Ancient World*. Cambridge, Cambridge University Press: 317-327.
- RODRÍGUEZ-PÉREZ H., FLORENCIO M., GÓMEZ-RODRÍGUEZ C., GREEN A. J., DÍAZ-PANIAGUA C. & SERRANO L. 2009 — Monitoring the invasion of the aquatic bug *Trichocorixa verticalis verticalis* (Hemiptera: Corixidae) in the wetlands of Doñana National Park (SW Spain). *Hydrobiologia* 634: 209-217.
- SALA J. & BOIX D. 2005 — Presence of the Nearctic water boatman *Trichocorixa verticalis verticalis* (Fieber, 1851) (Heteroptera, Corixidae) in the Algarve Region (S Portugal). *Graellsia* 61(1): 31-36.
- SANMARTÍN I. & RONQUIST F. 2004 — Southern Hemisphere biogeography inferred by event-based models: Plant versus animal patterns. *Systematic Biology* 53(2): 216-243.
- SCHUH R. T. & SLATER J. A. 1995 — *True bugs of the world (Hemiptera: Heteroptera) classification and natural history*. Cornell University Press, Ithaca, New York, 336 p.
- SCUDDER G. G. E. 1976 — Water-boatmen of saline waters (Hemiptera: Corixidae), in CHENG L. (ed.), *Marine Insects*. North-Holland Publishing Company, Amsterdam: 263-289.
- SHARMA P. & GIRIBET G. A. 2009 — A relict in New Caledonia: phylogenetic relationships of the family Troglosironidae (Opiliones: Cyphophthalmi). *Cladistics* 25: 279-294.
- SKUSE F. A. A. 1893 — Notes on Australian aquatic Hemiptera (n° 1). *Records of the Australian Museum* 2(4): 42-45.
- SPENCE J. R. & ANDERSEN N. M. 1994 — Biology of water striders: Interactions between systematics and ecology. *Annual Review of Entomology* 39: 101-128.
- ŠTYS P. 2008 — Zoogeography of Enicocephalomorpha (Heteroptera). *Journal of Insectology* 61: 137-138.
- TINERELLA P. P. 2008 — Taxonomic revision and systematics of New Guinea and Oceania pygmy water boatmen (Heteroptera: Corixidae: Micronectidae). *Zootaxa* 1797: 1-66.
- TURNER B., MUNZINGER J., DUANGJAI S., TEMSCH E. M., STOCKENHUBER R., BARFUSS M. H. J., CHASE M. W. & SAMUEL R. 2013 — Molecular phylogenetics of New Caledonian Diospyros (Ebenaceae) using plastid and nuclear markers. *Molecular Phylogenetics and Evolution* 69: 740-763.
- WHEELER W. C., SCHUH R. T. & BANG R. 1993 — Cladistic relationships among higher groups of Heteroptera: congruence between morphological and molecular data sets. *Insect Systematics & Evolution* 24(2): 121-137.
- WHITE F. B. 1883 — Report on the pelagic Hemiptera. *Voyage of Challenger, Reports, Zoology* 7: 1-82.
- YANG C. M. & MURPHY D. H. 2011 — Guide to the aquatic Heteroptera of Singapore and Peninsular Malaysia. 6. Mesoveliidae, with description of a new *Nereivelia* species from Singapore. *Raffles Bulletin of Zoology* 59(1): 53-60.
- ZETTEL H. 2004 — *Phrynovelia philippinensis* sp. n. (Heteroptera: Mesoveliidae) von der Insel Polillo, Philippinen. *Linzer Biologische Beiträge* 36(2): 1353-1358.
- ZETTEL H., LANE D. J. W., PANGANTIHON C. V. & FREITAG H. 2012 — Notes on Notonectidae (Hemiptera: Heteroptera) from south-eastern Asia, mostly from Brunei and the Philippines. *Acta Entomologica Musei Nationalis Pragae* 52(1): 29-48.

APPENDIX

Check-list of New Caledonian Gerromorpha & Nepomorpha.

GERROMORPHA Popov, 1971
MESOVELIIDAE Douglas & Scott, 1867

Austrovelia caledonica Malipatil & Monteith, 1983

TYPE LOCALITY — New Caledonia, Grande Terre: Mt. Rembai near Col d'Amieu.

DISTRIBUTION — Endemic to New Caledonia (Malipatil & Monteith 1983; Andersen 1999; Andersen & Polhemus 2003).

FIRST NC RECORD — Malipatil & Monteith (1983).

Mesovelis horvathi Lundblad, 1933

TYPE LOCALITIES — Indonesia: Java, Ranu Lamongan and Ranu Pakis /Sumatra, Lake Ranau.

DISTRIBUTION — From the south-eastern Palaearctic Region (China, Japan) throughout south-east Region (Clarify – south-east Asia? to Australia (Andersen & Weir 2004a) and New Caledonia.

FIRST NC RECORD — Known from a single female collected at Col d'Amou (Dec. 2008, J. Damgaard, ZMUC).

Mesovelis vittigera Horváth, 1895

TYPE LOCALITY — Egypt, Abukir and Cairo.

DISTRIBUTION — Southern Palaearctic, entire Ethiopian, Oriental, Malesian, and Australian Regions, eastwards to the Samoa, Guam and New Caledonia (Polhemus & Polhemus 2001).

FIRST NC RECORD — Polhemus & Herring (1970a, b).

Phrynovelia bimaculata Malipatil & Monteith, 1983

TYPE LOCALITY — New Caledonia, Grande Terre: Pic d'Amoa near Poindimié.

DISTRIBUTION — Endemic to New Caledonia (Malipatil & Monteith 1983; Andersen 1999; Andersen & Polhemus 2003).

FIRST NC RECORD — Malipatil & Monteith (1983).

Phrynovelia caledonica Malipatil & Monteith, 1983

TYPE LOCALITY — New Caledonia, Grande Terre: Mt. Panié.

DISTRIBUTION — Endemic to New Caledonia (Malipatil & Monteith 1983; Andersen 1999; Andersen & Polhemus 2003).

FIRST NC RECORD — Malipatil & Monteith (1983).

HYDROMETRIDAE Billberg, 1820

Hydrometra aculeata Montrouzier, 1864

TYPE LOCALITY — New Caledonia.

DISTRIBUTION — Endemic to New Caledonia (Polhemus & Lansbury 1997).

FIRST NC RECORD — Montrouzier (1864).

Hydrometra strigosa (Skuse, 1893)

TYPE LOCALITY — Australia, New South Wales: Botany Swamps.

DISTRIBUTION — Australia and adjacent islands (Norfolk Is., Lord Howe Is.), Vanuatu, New Zealand, and Tahiti of the Society Is. (Andersen & Weir, 2004a; Buzzetti *et al.*, 2006).

FIRST NC RECORD — Hungerford (1938) (as *H. ribescii*).

HERMATOBATIDAE Coutière & Martin, 1901

Hermatobates armatus Andersen & Weir, 2000

TYPE LOCALITY — New Caledonia, Chesterfield Islands: Bennette & Long Island (HT).

DISTRIBUTION — Endemic to New Caledonia.

FIRST NC RECORD — Andersen & Weir (2000).

Hermatobates marcheï (Coutiere & Martin, 1901)

TYPE LOCALITY — Philippines: Ile Paragua, Baie de Honda.

DISTRIBUTION — widely distributed along the coasts of the western Pacific, from southern Japan to Australia, Fiji, and Tonga (Andersen & Weir 2004a).

FIRST NC RECORD — Andersen & Weir (2000).

VELIIDAE Amyot & Serville, 1843

Halovelvia bergrothi Esaki, 1926

TYPE LOCALITY — Papua New Guinea: Berlinhafen, Seleu.

DISTRIBUTION — Widespread in the Oriental, Malesian and Pacific Regions (Chen *et al.*, 2005).

FIRST NC RECORD — Andersen (1989).

Halovelvia hilli China, 1957

TYPE LOCALITY — Australia, Western Australia: Monte Bello Is., S. Hermite.

DISTRIBUTION — East Timor, New Guinea, Australia (Andersen & Weir 2004a).

FIRST NC RECORD — Andersen (1989).

Xenobates loyaltiensis (China, 1957)

TYPE LOCALITY — New Caledonia: Uvea, Fayaoye Bay.

DISTRIBUTION — Endemic to New Caledonia (Andersen & Weir 1999).

FIRST NC RECORD — China (1957).

Microvelia (Pacifcovelia) oceanica Distant, 1914

TYPE LOCALITY — New Caledonia, Grande Terre: Outbache.

DISTRIBUTION — Australia and adjacent islands (Lord Howe I., Norfolk I.), Vanuatu, Fiji (Andersen & Weir, 2004a).

FIRST NC RECORD — Distant (1914).

Microvelia (Pacifcovelia) starmuehlneri Polhemus & Herring, 1970a, b

TYPE LOCALITY — New Caledonia, Grande Terre: Mt. Dogny.

DISTRIBUTION — Endemic to New Caledonia (Andersen & Weir 2003).

FIRST NC RECORD — Polhemus & Herring (1970a, b).

Rhagovelia novacaledonica Lundblad, 1936

TYPE LOCALITY — New Caledonia, Grande Terre: Mt. Ignambi.

DISTRIBUTION — Endemic to New Caledonia (Polhemus & Polhemus 1988).

FIRST NC RECORD — Distant (1914) (as *Rhagovelia nigricans* (Burmeister 1835)).

Rhagovelia pidaxa Polhemus & Herring, 1970a, b

TYPE LOCALITY — New Caledonia, Grande Terre: Mt. Dogny.

DISTRIBUTION — Endemic to New Caledonia (Polhemus & Polhemus 1988).

FIRST NC RECORD — Polhemus & Herring (1970a, b).

GERRIDAE Leach, 1815

Halobates germanus White, 1883

TYPE LOCALITY — North Pacific Ocean.

DISTRIBUTION — Indian Ocean, Red Sea, West and Central Pacific Ocean (Andersen & Cheng 2004).

FIRST NC RECORD — Herring (1961).

Halobates katherinae Herring, 1958b

TYPE LOCALITY — New Caledonia, Grande Terre: Nouville.

DISTRIBUTION — Vanuatu and New Caledonia (Andersen & Cheng 2004).

FIRST NC RECORD — Herring (1958b).

Halobates panope Herring, 1961

TYPE LOCALITY — New Caledonia, Grande Terre: stream estuary between Touho and Ponerihouen.

DISTRIBUTION — Endemic to New Caledonia (Andersen & Cheng 2004).

FIRST NC RECORD — Herring (1961).

Halobates sericeus Eschscholtz, 1822

TYPE LOCALITY — North Pacific.

DISTRIBUTION — Pacific Ocean between 40°N and 5°N and between 5°S and 40°S (Andersen & Weir 2004a).

FIRST NC RECORD — Herring (1961).

Limnogonus fossarum gilguy Andersen & Weir, 1997

TYPE LOCALITY — Australia, Queensland: Burster Creek.

DISTRIBUTION — Malesian Region (Java), Australia, Vanuatu, Fiji, Samoa, Cook Islands (Andersen & Weir 2004a).

FIRST NC RECORD — Polhemus & Herring (1970a, b).

Limnogonus luctuosus (Montrouzier, 1864)

TYPE LOCALITY — New Caledonia, Grande Terre: Kanala.

DISTRIBUTION — Probably endemic to New Caledonia (Damgaard *et al.* 2010). Records from Australia, Solomon Is., Vanuatu, Fiji, Samoa, Society Islands (Andersen & Weir 2004a) are likely to represent undescribed species.

FIRST NC RECORD — Montrouzier (1864) (as *Gerris luctuosa* Montrouzier 1864).

NEPOMORPHA Popov, 1971
BELOSTOMATIDAE Leach, 1815

Lethocerus insulanus (Montandon, 1898)

TYPE LOCALITY — Probably New Caledonia.

DISTRIBUTION — Australia (NSW, NT, QLD), New Guinea (Andersen & Weir 2004a; Chen *et al.* 2005).

FIRST NC RECORD — Montandon (1898).

GELASTOCORIDAE Kirkaldy, 1897

Nerthra kerzhneri Cassis & Silveira, 2006

TYPE LOCALITY — New Caledonia, Grande Terre: Port Boise.

DISTRIBUTION — Endemic to New Caledonia (Cassis & Silveira 2006)

FIRST NC RECORD — Cassis & Silveira (2006).

OCHTERIDAE Kirkaldy, 1815

Ochterus australicus Jaczewski, 1934

TYPE LOCALITY — New Caledonia, Grande Terre: Gondé, Hovailov River.

DISTRIBUTION — Australia, Vanuatu, Solomon Is. (Baehr 1989).

FIRST NC RECORD — Jaczewski (1934) without date according to Polhemus & Herring (1970a, b)

Ochterus dufourii (Montrouzier, 1864)

TYPE LOCALITY — New Caledonia, Grande Terre: Kanala.

DISTRIBUTION — Endemic to New Caledonia (Baehr 1989).

FIRST NC RECORD — Montrouzier (1864) (as *Pelogonus dufourii*, Montrouzier 1864).

CORIXIDAE Leach, 1815

Sigara (Tropocorixa) tadeuszi Lundblad, 1933

TYPE LOCALITY — Australia, New South Wales: Manly, Sydney.

DISTRIBUTION — New Guinea, Australia (NSW, QLD, SA) (Andersen & Weir 2004a; Chen *et al.* 2005).

FIRST NC RECORD — Polhemus & Herring (1970a, b).

Sigara (Tropocorixa) truncatipala (Hale, 1922)

TYPE LOCALITY — Australia, South Australia: Adelaide.

DISTRIBUTION — New Guinea, Australia (NSW, QLD, SA, TAS, VIC, Lord Howe I.) (Andersen & Weir 2004a; Buzzetti *et al.* 2006; Chen *et al.* 2005).

FIRST NC RECORD — Polhemus & Herring (1970a, b).

Trichocorixa verticalis verticalis (Fieber, 1851)

TYPE LOCALITY — U.S.A. (Pennsylvania).

DISTRIBUTION — Native to the Atlantic coast of the United States, coastal areas of Mexico, and in the Caribbean Islands. Introduced to South Africa (Jansson & Reawell 1999) south-western Europe (Portugal, Spain) (Sala & Boix 2005; Rodríguez-Pérez *et al.* 2009).

FIRST NC RECORD — Jansson (1982).

PLEIDAE Fieber, 1851

Paraplea liturata (Fieber, 1844)

TYPE LOCALITY — India.

DISTRIBUTION — Oriental Region, Malesian Region, Australia (Andersen & Weir 2004a; Chen *et al.* 2005).

FIRST NC RECORD — Distant (1914) (as *Plea rufonota* Distant, 1914).

NOTONECTIDAE Latreille, 1802

Enithares bergrothi Montandon, 1892

TYPE LOCALITY — New Caledonia.

DISTRIBUTION — Endemic to New Caledonia (Lansbury 1968).

FIRST NC RECORD — Montandon (1892).

Anisops cleopatra Distant, 1914

TYPE LOCALITY — New Caledonia, Grande Terre: near Koné

DISTRIBUTION — Sumatra, Java, Guam, New Caledonia, Samoa (Brooks 1951).

FIRST NC RECORD — Distant (1914).

Anisops crinitus Brooks, 1951

TYPE LOCALITY — Greece (Corfu).

DISTRIBUTION — Widespread in the southern Palearctic and western Oriental Regions, an isolated record from New Caledonia (Brooks 1951).

FIRST NC RECORD — Brooks (1951) (as *A. crinita* Brooks, 1951).

Anisops hyperion Kirkaldy, 1898

TYPE LOCALITY — Australia, Queensland: Rockhampton.

DISTRIBUTION — Widespread in the Oriental and Australian Regions (Andersen & Weir 2004a).

FIRST NC RECORD — Lundblad (1933).

Anisops occipitalis Breddin, 1905

TYPE LOCALITY — Indonesia, Java: Buitenzorg.

DISTRIBUTION — From China and southern Japan (Ryu Kyu Is.) via southeastern Asia and the Malay archipelago to Australia and New Guinea (Zettel *et al.* 2012).

FIRST NC RECORD — Brooks (1951).

New Caledonia as an evolutionary cradle: a re-appraisal of the jaw-moth genus *Sabatinca* (Lepidoptera: Micropterigidae) and its significance for assessing the antiquity of the island's fauna

George W. Gibbs⁽¹⁾ & David C. Lees⁽²⁾

⁽¹⁾ School of Biological Sciences, Victoria University, Wellington, New Zealand
george.gibbs@vuw.ac.nz

⁽²⁾ Department of Zoology, Cambridge University, Cambridge, UK
dl490@cam.ac.uk; dclees@gmail.com

ABSTRACT

Current literature indicates the presence of the archaic moth family Micropterigidae on New Caledonia but gives little indication of its diversity and significance. By 1985, three species of the genus *Sabatinca* had been described for the island. In 2010, a further two species in two new genera were added. Recent fieldwork has revealed species richness greater than that of the northern and central European fauna of *Micropterix* (the genus with most described species in this family). Their diversity and evolution on an emergent SW Pacific island whose age and previous land connections are hotly debated, provides a fascinating challenge in historical biogeography with the potential to illuminate the age and history of inundation of the island and its past geological setting. On-going taxonomic research reveals at least 55 species in three genera on the island, with relationships to both Australia and New Zealand. COI DNA barcoding indicates that the New Caledonian fauna represents two of the five major lineages in the family —the Australian lineage, poorly represented with two described species; and the *Sabatinca* lineage whose type species is New Zealandian, with a highly diverse New Caledonian radiation (~33 taxa analysed so far). These new molecular data lead to a reassessment of the phylogenetics of the genus *Sabatinca* and the previous use of the term 'sabatincoid'. The main taxonomic outcome is to present a subdivision of *Sabatinca* into three informal species groups: 1) an *incongruella* group, which includes two New Zealand species and all those known from New Caledonia; 2) a *chrysargyra* group, and 3) a *calliarcha* group, the last two confined to New Zealand. We provide diagnostic morphological and molecular characters for the three monophyletic groups recognised within the *Sabatinca* lineage. COI indicates that the New Caledonian

lineage has been derived from an earlier diversification of the *Sabatinca* species group in New Zealand. Our Beast dating analysis, constrained by non-sabatincan micropterigid and trichopteran fossil calibrations, implies that radiations of the clearly monophyletic genus *Sabatinca* started at around 84 Ma, with the New Caledonian radiation at *ca.* 52 Ma and New Zealand *chrysargyra* group at *ca.* 50 Ma. Both dates are long before the widely accepted ages of the modern islands following their respective 'drowning events'. The radiation of both the *Sabatinca* lineage and the New Zealand/New Caledonia components of the Australian group lineage are largely compatible with a vicariant trans-Tasman history.

RÉSUMÉ

La Nouvelle-Calédonie en tant que berceau évolutif : une mise au point sur les papillons mandibulés du genre *Sabatinca* (Lepidoptères : Micropterigidae) et son apport à l'évaluation de l'ancienneté de la faune de l'île.

Les données publiées à ce jour indiquent la présence en Nouvelle-Calédonie de la famille des Micropterigidae (papillons archaïques), mais ne permettent guère d'évaluer — a fortiori d'interpréter — sa diversité. Fin 1985, seules trois espèces de *Sabatinca* avaient été décrites de l'île. En 2010, deux autres espèces ont été ajoutées à la liste, espèces se rattachant à deux genres nouveaux. Des missions de terrain récentes ont révélé une richesse en espèces supérieure à celle des *Micropterix* du nord et du centre de l'Europe (*Micropterix* étant le genre le plus riche de la famille). En considérant la diversité et l'évolution de Micropterigidae sur une île (émergée) du sud-ouest du Pacifique dont l'âge et les connexions terrestres passées font l'objet de vifs débats, on est confronté à un formidable défi en matière de biogéographie historique, avec la possibilité d'établir l'âge et le passé géologique de l'île, ainsi que l'histoire de ses phases de submersion. Les investigations taxonomiques en cours révèlent l'existence sur l'île d'au moins 55 espèces réparties en trois genres, faune dont les affinités sont à la fois australiennes et néo-zélandaises. L'étude en cours des codes-barres ADN (marqueur : COI) montre que deux des cinq grandes lignées de Micropterigidae sont présentes en Nouvelle-Calédonie : la lignée australienne, pauvrement représentée (avec deux espèces décrites) et la lignée des *Sabatinca* (dont l'espèce-type est néo-zélandaise), avec une radiation néo-calédonienne très diversifiée (environ 33 taxons analysés à ce jour). Ces nouvelles données moléculaires permettent de réévaluer la phylogénie du genre *Sabatinca* et l'utilisation antérieure du terme « sabatincoïde ». Nous proposons une subdivision du genre *Sabatinca* en trois groupes d'espèces : 1) le groupe *incongruella* comprenant deux espèces néo-zélandaises et toutes les espèces connues de Nouvelle-Calédonie, 2) le groupe *chrysargyra* et 3) le groupe *calliartha*, ces deux derniers confinés en Nouvelle-Zélande. Nous donnons des caractères morphologiques et moléculaires permettant de définir ces trois groupes monophylétiques mis en évidence au sein de la lignée des *Sabatinca*. Le marqueur COI indique aussi que la lignée néo-calédonienne dérive de la diversification néo-zélandaise — plus ancienne — des *Sabatinca* sensu lato. Avec le logiciel BEAST (en prenant, pour l'étalement, des Microptéridés autres que les *Sabatinca*, ainsi que des Trichoptères fossiles), notre analyse suggère que la radiation du genre *Sabatinca* — un groupe clairement monophylétique — a commencé il y a environ 84 Ma, la radiation néo-calédonienne il y a environ 52 Ma et celle du groupe néo-zélandais *chrysargyra* il y a environ 50 Ma. Dans ces deux cas, il s'agit d'une ancienneté excédant largement l'âge habituellement envisagé pour les îles en question (en considérant la période ayant fait suite à leurs « événements de submersion »). La radiation de la lignée des *Sabatinca* et celle des éléments néo-zélandais et néo-calédoniens de la lignée australienne s'interprètent assez bien, l'une et l'autre, dans le cadre d'un scénario de vicariance trans-tasmanienne.

INTRODUCTION

New Caledonia is becoming known for its species-richness and high level of endemism in certain of its fauna and flora (Muriénne 2009). Explanations for this remarkable diversity have escalated recently as phylogenetic research on its biota intensifies (Grandcolas *et al.* 2008, Muriénne *et al.* 2005, Muriénne 2009). There is now an ever-increasing number of advocates for discarding the 'classical' view of a Gondwanan refuge where archaic groups have survived for 60–80 million years (Ma) (*e.g.* Holloway 1979, Morat 1993, Heads 2008), and replacing it with the idea of a 'large Darwinian island' concept, populated since 37 Ma by trans-oceanic dispersal (Grandcolas *et al.* 2008). A third possibility, namely that it could be both of the above, as seems to be the case with New Zealand (Giribet & Boyer 2010), depending on which component of the biota is being studied, has not received the consideration it deserves. The New Caledonian debate is running in parallel with the so-called 'Moa's Ark' controversy over New Zealand's biotic antiquity (*e.g.* Tennyson *et al.* 2010 vs Wallis & Trewick 2009) which is particularly relevant since both of the present land masses represent emergent fragments of the

93% submerged continent Zealandia (Mortimer 2004). We contend that generalisations based on insufficient case studies can be misleading until sufficient phylogenetic data accrue to enable a more balanced overview. The present contribution is a progress report on a study which has the potential to address that issue.

The insects of interest here (Micropterigidae) are small archaic moths with almost 'ideal' characteristics for historical biogeographic research. First, they have a deep fossil record that illustrates their antiquity and to some degree supports the contention that they have remained essentially unchanged since early Cretaceous, certainly with respect to morphology and very possibly in relation to their humid forest habitat also. We know that these pre-angiosperm moths (micropterigids are dependent mainly on liverworts as larvae and fern spores or in a few cases angiosperm pollen as adults: Imada *et al.* 2011) were well established at the time Gondwana was breaking up and were abundant enough to become trapped in resinous exudates of Araucarian trees (amber) of that era. The earliest indisputable fossil micropterigid, perfectly preserved in Lebanese amber (Whalley 1978), is datable to about 136 Ma (Azar *et al.* 2002) and is followed by 93–100 Ma amber fossils from Myanmar (Grimaldi & Engel 2005; see Gibbs 2010) and Spain (Delclòs *et al.* 2007). Second, their present-day distribution, on continents or former fragments of older continents, provides a virtually worldwide geographical picture —extremely useful for interpreting their overall evolutionary history (Mey 2011). Third, their world phylogeny resolves five main lineages, each confined to discrete geographical regions with cases of lineage overlap being largely explicable by tectonic events (Gibbs *et al.* 2004; Gibbs 2006). The SW Pacific (*i.e.* Eastern Australia, New Caledonia, New Zealand) has emerged as the most interesting region globally, where three of the five lineages intersect on the emergent lands surrounding the Tasman Sea.

Existence of the primitive lepidopteran family Micropterigidae in New Caledonia was first revealed during a 1971 Lepidoptera survey by Jeremy Holloway (Whalley 1978, Holloway 1979). In 1978, Viette described the nocturnal *Sabatinca delobeli* from four specimens taken near Nouméa in November–December 1976 (Viette 1978). Two additional species, both diurnal, were added by Minet (1985). Three parties of entomologists with a lepidopteran focus have intensively sampled the fauna in 1978 (JS Dugdale, NZDSIR), 1984 (M Pogue and M Epstein, USNM), and 1986 (R Brown and O Pellmyr, USNM). This field work, together with six visits by GWG has resulted in approximately 1200 specimens available for the present study. The collections have revealed a richness on this SW Pacific island which is greater than that of *Micropterix* (as yet the most species-rich genus of this family) throughout the whole of northern and central Europe, where 49 of an estimated 79 species occur (Zeller-Lukashort *et al.* 2007; Lees *et al.* 2010b).

Long-standing taxonomy (from Walker 1863 and summarised in Dugdale 1988), has placed the entire SW Pacific micropterigid fauna in the genus *Sabatinca* Walker 1863, with the exception of two New Zealand taxa in the genus *Micropardalis* Meyrick 1912 —a taxonomy which obscures the natural groupings and significance of these moths for biogeographic interpretation. Gibbs (1983) drew attention to the distinction between the 'sabatincoïd' taxa and the 'Australian group' of taxa in this region. The former included all *Sabatinca* species of New Caledonia and New Zealand, together with *Austromartyria porphyrodes* (Gibbs 2010) from northern Queensland whereas the latter referred to eight species from eastern Australia, two from New Caledonia and one from New Zealand, all of which had been included within the genus *Sabatinca* at that time but clearly required taxonomic revision to recognise their distinctive morphological features. Now, with revised taxonomy of the latter group (Gibbs 2010), and with molecular phylogenetic support (Gibbs *et al.* 2004), the biogeographic range of the *Sabatinca* lineage of Micropterigidae is found to be confined to islands on the Zealandia continental plate, with 18 species in New Zealand and upwards from 55 in New Caledonia.

Thus, Holloway's statement, with reference to the New Caledonian Lepidoptera fauna, that 'there are no old connections with New Zealand' (Holloway 1979: 222) may fit the macrolepidopterans but is certainly no longer appropriate for microlepidopterans where a single archaic genus can demonstrate that New Caledonia indeed represents a 'cradle of evolution' (*sensu* McKenna & Farrell 2006) for the Zealandian genus *Sabatinca*. The evolutionary exuberance of *Sabatinca* that exists on the island is in marked contrast to the presence of only two described 'Australian group' taxa (*Aureopterix micans* and *Nannopterix choreutes*: Gibbs, 2010), a fauna which could be considered to represent no more than a 'museum of ancient diversity' (*sensu* McKenna & Farrell 2006). The goals of the present research are to provide another case study on the origin of New Caledonia's fauna and to offer a first phylogenetic framework for the *Sabatinca* lineage of Micropterigidae. A formal taxonomic revision is being prepared, hence this paper represents an interim report on work in progress.

Note that an arbitrary system of species numbers (sp. 1 – sp. 53) has been employed (by GWG) when referring to the undescribed taxa of New Caledonian Micropterigidae.

MATERIAL AND METHODS

We amplified barcodes from single adult leg extractions produced by Barcode of Life Data Systems (BOLD) (Ratnasingham & Hebert 2007) of up to 658 bp using primers Lep-F1 and Lep-R1 and in a few cases where these did not work 307 bp using LepF1/MLepR1, according to standard protocols at CCDB (http://www.ccdb.ca/docs/CCDB_Amplification.pdf). Vouchers can be viewed at the BOLD website (<http://www.barcodinglife.com/views/taxbrowser.php?taxid=587>) and are fully documented therein. Genbank numbers, taxonomy and geographic data of individuals sequenced are provided in Appendix 1 and in the cases where Genbank numbers are lacking, partial barcodes are still available as public data in the project MICA of BOLD (http://www.boldsystems.org/index.php/MAS_Management_ProjectList#WG1.9%20Terrestrial%20Bio-Surveillance). We added data where relevant from the work of Imada *et al.* 2011 where the COI region shows partial overlap (Figure 7). Alignment was straightforward by eye and via codon conversion in Bioedit v. 1.07 (Hall 1999).

For the species diversity and phylogenetic analysis of *Sabatinca*, we used a MrBayes 3.1 (Ronquist and Huelsenbeck 2003) analysis to infer the phylogenetic relationships of 88 terminals including 59 New Caledonian exemplars of *Sabatinca*, and all described species of the *Sabatinca chrysargyra* group and of the *calliarcha*-group, rooted by *Austromartyria porphyrodes*. Where possible we included up to three examples of each species/morphospecies (and also a sequence of *S. viettei* from the work of Imada *et al.* 2011). We ran this analysis partitioned between (1st and 2nd), and 3rd codon positions respectively, under a GTR + I + gamma model for 12,500,000 generations with a burnin of 10%, to arrive at a standard deviation of split frequencies below 0.01, checking that both runs had achieved convergence.

For the dating analysis, a subset of 67 micropterigid taxa (including a sample of 30 *Sabatinca* species) was used. In order to allow a reasonable calibration of the base of amphiesmenopteran tree rather than constraining the root to an arbitrary age, we included also twelve trichopteran outgroups (four of which are *Rhyacophila*, to represent the high COI variability/potential antiquity of this genus). We did not include other primitive Lepidoptera due to the lack of suitable fossils for calibration. We set up a BEAST run using BEAUti 1.4.8 (Drummond and Rambaut 2007) to produce, as for MrBayes 3.1, a partitioned bayesian analysis (GTR model + Invariant sites + gamma; 1st + 2nd and 3rd positions as separate partitions, all parameters unlinked across codon positions), constrained by minimum age fossil data. We used 37 Ma (rather than ~44–55 Ma for Baltic amber as cautioned by Perkovsky *et al.* 2007), to constrain the minimum age of the *Micropterix* crown group (fossil record summarized in Lees *et al.* 2010b); 96.5 Ma for Burmese Amber (the midpoint of the Cenomanian age suggested by Grimaldi *et al.* 2002) for the minimum age of the crown group including *Tasmantrix*, *Zealandopterix* and *Aureopterix*: based on the fossil illustrated in Grimaldi & Engel 2005: 562, Fig. 13.17, AMNH Bu701 (here considering tentatively its wing venational characters to be evidence of group membership: see Gibbs 2010); 136 Ma as the lower 95% confidence interval for the Micropterigidae crown group (based on the Lebanese amber fossil *Parasabatinca aftimacraei*: Whalley 1978). Among trichopterans, we used as minimum age constraints, 185 Ma for the earliest fossil that is clearly trichopteran, *Liadotaulius maior* (Ansorge 2003, Grimaldi & Engel 2005); 168 Ma for the minimum age of the split of Philopotamidae (one middle Jurassic fossil, *Juraphilopotamus lubricus*: Wang *et al.* 2009) and its sister group Stenopsychidae; 96.5 Ma for the minimum age of the Rhyacophilidae crown group based on the fossil *Rhyacophila antiquissima* Botosaneanu & Wichard, 1983, from the Upper Cretaceous possibly Cenomanian: (Grimaldi *et al.* 2002) amber of Taimyr, Siberia (a fossil also used for calibration by Strandberg & Johanson 2010); 150 Ma for the split between Rhyacophilidae and Hydrobiosidae (based on the latter family from the late Jurassic of Mongolia according to Ivanov & Sukatsheva 2002, as illustrated in Grimaldi & Engel 2005: 553). As a prior for mean rate, we used 0–0.05 substitutions per site per Ma and for the variance 0–0.025 (as in Lees *et al.* 2010b). All other priors had default initial settings. Groups with fossil estimates applied were constrained as monophyletic and we used a random coalescent starting tree and a Yule prior speciation model. As determined by achieving an adequate ESS in Tracer 1.5 (>100 for any parameter), we ran the MCMC chain for 12,500,000 generations in BEAST v 1.6.1 (Drummond and Rambaut 2007) with a burnin of 25% before summarizing the tree in TreeAnnotator v. 1.6.1 (all software from <http://beast.bio.ed.ac.uk>).

TAXONOMIC PART

VALUE OF THE TERM 'SABATINCROID'

A molecular phylogenetic evaluation of a large number of new taxa from New Caledonia, using the barcode region of COI (which in Micropterigidae is known to provide support for deep splits: Lees *et al.* 2010b), has been able to shed some light on the long-standing question of a more appropriate taxonomic classification for the *Sabatinca* lineage which was established with regard to the New Zealand taxa. The dominance of this genus on the two major emergent islands of the continental plate Zealandia (*i.e.* New Zealand and New Caledonia), and its apparent absence from the continent of Australia, together with its molecular distance (Gibbs 2006) from the Australian lineage (as defined by Gibbs 2010), indicates that there has been a major and very early separation between two monophyletic evolutionary lineages of Micropterigidae in the SW Pacific. This is the only region world-wide where three major micropterigid lineages overlap today: 1) the Australian lineage, 2) the *Sabatinca* lineage, and 3) the circum-global 'southern sabatinroid' lineage (Gibbs 2010). Although the faunal barcoding is still 'in progress', we use this opportunity to review our concept of genus *Sabatinca* and the 'sabatinroid group' of taxa with some new enlightenment from the diverse New Caledonian fauna.

Molecular evidence from a mitochondrial 16S *r*RNA dataset has defined a monophyletic *Sabatinca* clade supported as one of the five lineages within the family (Gibbs *et al.* 2004; Gibbs 2006: 97). This lineage is comprised solely of taxa from New Caledonia and New Zealand and includes all micropterigid species (approximately 70) currently known from these islands, apart from the three species assigned to the Australian lineage by Gibbs 2010. The third lineage in the SW Pacific overlap area is represented by the monotypic genus *Austromartyria* Gibbs, from North Queensland (Gibbs 2010). This latter taxon is a member of a much more widespread lineage that occurs around the southern hemisphere, with species in southern Africa, Madagascar, Australia, Chile, and possibly Costa Rica and Ecuador and has been dubbed the 'southern sabatinroid' group by Gibbs (2010), and Gibbs & Kristensen (2011).

The term 'sabatinroid' was first coined by Kristensen & Nielsen (1979) to differentiate between *Micropterix* and all other members of the family, distributed over both hemispheres. Since then the term has been applied loosely in this sense. Minet (1985) reviewed its value in association with his description of two species from New Caledonia, concluding that we resort to it as the last stand of a working hypothesis, but certainly not as evidence for an indisputable monophyletic group. In the light of the molecular evidence and the study of many undescribed new taxa, our current interpretation of relationships largely concurs with this view. It is best summarised with reference to the five-lineage phylogenetic interpretation of Micropterigidae which has emerged and although its topology is so far unsettled (Gibbs 2006; 2010) the discreteness of all five lineages has been corroborated by all genes analysed to date (Lees *et al.* 2010a). As our understanding of the family as a whole has improved, the scope of the term 'sabatinroid' has been diminished by the removal of two additional non-*Micropterix* lineages — a northern hemisphere Asia-North America lineage centred on eastern Asia (*Paramartyria*, *Issikiomartyria*, *Kurokoptyx*, *Palaeomicrodes*, and *Vietomartyria*) and North America (*Epimartyria*) (Hashimoto 2006; Davis & Landry 2012); and the Australian lineage discussed above (*Tasmantrix*, *Aureopterix*, *Nannopterix* and *Zealandopterix*) (Gibbs 2010). The result is that at most only two of the five lineages can now qualify to be called 'sabatinroid', both essentially southern: one with a circum-southern distribution and a main concentration in the Afrotropical region (the 'southern sabatinroid' lineage) (Gibbs & Kristensen 2011); and the other confined to New Zealand and New Caledonia (the *Sabatinca* lineage).

Ignoring fossil history, 'sabatinroid' in the last sense seems to make geographic sense but defining autapomorphies are elusive, implying that the concept might be paraphyletic/polyphyletic. The grouping is supported in adults by the sharing of an external morphology for the abdominal segment 5 gland orifice, which lies on a roughly circular elevated protuberance from which a number of long piliform setae arise. By contrast, in the *Micropterix* lineage, the gland is lost: while in the east Asian/N. American lineage the gland orifice is 'naked', on a scale-like area and lacks piliform setae. However, in the Australian lineage (*Tasmantrix* and allies) both types can occur, even differing between sexes within a species.

The term 'sabatinroid' has also been applied to a larval morphotype. It refers to the unique type of lepidopteran larva, first described by Tillyard (1923) for a New Zealand species, *Sabatinca barbarica*, characterised by its hunch-backed,

slug-like form, with pronounced dorsal and lateral longitudinal ridges giving it a hexagonal cross-section. These larvae are exposed liverwort-feeders (like many Asian species: Imada *et al.* 2011), with a thick honeycombed integument, pigmented for crypsis. There are eight pairs of spiracles, three pairs of greatly reduced thoracic legs and usually no abdominal prolegs. However, this concept is not congruent with adults as 'sabatincoïd' larvae occur not only in the *Sabatinca* lineage and the 'southern sabatincoïd' lineage, but also in the Asian/North American lineage (Tuskes & Smith 1984, Hashimoto 2006, Imada *et al.* 2011). The latter are distinguished from southern sabatincoïd larvae by the position of the abdominal spiracles in the intersegmental grooves, rather than at mid-segment.

The alternative larval morphotype, for which the term 'micropteroid' may be coined, is the form known for both *Micropterix* and the Australian lineages. These larvae are unpigmented, subterranean and roughly circular or oval in cross section, with longitudinal furrows and seven pairs of spiracles situated in the middle of the abdominal segments. The thoracic legs are longer (although still very short), abdominal prolegs are present on all segments, and they are deemed to be fungal or detrital feeders, although some have been reared on seedling angiosperms (Carter & Dugdale 1982).

The above discussion suggests that because the term 'sabatincoïd' can be variously applied as a descriptor for traits spanning different lineages, it has limited value in systematic discussions and must in future be qualified.

From an evolutionary perspective, if not as a result of inadequate sampling effort (Kristensen *et al.* 2007), there is a striking contrast between the southern sabatincoïd lineage—which is thought to represent surviving fragments of a very wide relictual group, ranging from South Africa through Australia to Chile—and the diverse species-rich *Sabatinca* lineage confined to New Caledonia and New Zealand. The diversity of this latter group parallels the large radiations in the two northern lineages: the Asian/N American lineage of 37 valid described species (Hashimoto 2006; Hirowatari *et al.* 2009; Davis & Landry 2012), and the Eurasian *Micropterix* lineage of 74 valid described species (Zeller-Lukashort *et al.* 2007; Lees *et al.* 2010b). While the northern groups are highly conservative in terms of their overall colour and maculation, the *Sabatinca* group could be described as exuberantly colourful and diverse.

To view the New Caledonian fauna in a taxonomic context, it is necessary to first consider the genus-level taxonomy of the New Zealand micropterigid fauna, and the previous attempts to define it. Three genera have been established for the New Zealand species: *Sabatinca* Walker 1863 (type species *incongruella*), *Palaeomicra* Meyrick 1885 (type species *chrysargyra*), and *Micropardalis* Meyrick 1912 (type species *doroxena*). An interpretation by Minet (1985) supports retention of these three taxa but at subgeneric level and is founded largely on genitalic characters and the condition of forewing veins Rs3 & 4. On the other hand, Dugdale (1988), in his catalogue of the New Zealand Lepidoptera fauna, retains *Sabatinca* for all taxa except two species of *Micropardalis* (*doroxena* and *aurella*). What can the molecular evidence tell us? And how best should the New Caledonian fauna be incorporated into a revised taxonomy, if one is indeed necessary?

TAXONOMIC IMPLICATIONS FOR THE SABATINCA LINEAGE

The phylogenetic analysis, recovered from COI 'barcode' determination of 14 species from New Zealand and about 33 species from New Caledonia all within the *Sabatinca* lineage as defined here, delineates about 47 species for three monophyletic clades each supported by a posterior probability of 0.99-1.0 (see Figures 6, 7 below).

- 1) *S. incongruella* clade—which includes all the known described and undescribed New Caledonian sabatincoïd taxa except *Aureopterix* and *Nannopterix* Gibbs, 2010. Note that this clade includes two New Zealand species (*incongruella* and *demissa*) at its base, a total of more than 55 species.
- 2) *S. chrysargyra* clade, which includes 11 species restricted to New Zealand (two of which are currently undescribed) and which are readily distinguishable by morphological autapomorphies in both adult and larval stages.
- 3) *S. calliarcha* clade, a group of five New Zealand *Sabatinca* species (*calliarcha*, *lucilia*, *heighwayi* and two undescribed species), which appear in molecular analyses either as a sister to *S. chrysargyra* clade or as a basal sister clade to both the above clades. COI barcodes reveal several diagnostic molecular characters including at amino acid level (see below) but only weakly-supported morphological autapomorphies (e.g. larval chaetotaxy), to serve as markers.

Because of the instability of the *calliarcha* group in molecular reconstructions and the interim status of this report pending a full systematic treatment, we consider that it would be premature to formalise the three clades taxonomically

at this stage, especially on the basis of a single gene analysis. The following descriptive treatment of the three clades is therefore included here to relate morphology to molecular differentiation and to illustrate how the New Caledonian radiation sits within the concept of a *Sabatinca* lineage.

Family MICROPTERIGIDAE Herrich-Schaffer, 1855

Genus ***SABATINCA*** Walker, 1863

Sabatinca Walker, 1863: 511

Type species. *Sabatinca incongruella* Walker, 1863 by monotypy.

MORPHOLOGICAL DIAGNOSIS — Head and thorax with tufts of very long piliform scales on frons, vertex, scape, pedicel, tegulae, mesoscutum and mesoscutellum; Antennal ascoids with branches arising radially around a near-circular base; forewing (FW) veins Sc and R deeply forked; hindwing (HW) vein R either discrete distad from 'typical' R/Rs fork and eventually anastomosing with subapical part of Sc2, or lacking an R vein, which appears only as a small proximally-directed 'spur' from Sc2; vein Rs with four branches (see Figure 2 below); protibia with well-developed epiphysis; sternum 5 gland orifice on a raised peduncle in both sexes, bearing a number of long piliform scales (2-16); male sternite 8 never independent; medioventral length of male vinculum longer than length of sternite 6 (1.2-4.9x medioventral length of sternite 6), with a wide and conspicuously melanised anteromarginal sulcus; male tergum 10 with median lobe or bilobed, but undivided on anterior part. Larvae typically 'sabatinoid', *i.e.* 'hunch-backed' liverwort-feeders, with a single macroscopic D seta (D1) on T3 and a single L seta on A1-7 (see Figure 8C below).

MOLECULAR DIAGNOSIS — Threonine (T) rather than Proline (P) in the 212th complete codon of the COI barcode, representing a first positional A rather than C in the 635th nucleotide position; this unreversed character change is unique to our knowledge not only among micropterigids - but among amphiesmenopterans - for which a C is otherwise invariant at this nucleotide position.

COMPARATIVE NOTES (*SABATINCA* LINEAGE) — **General facies.** The diversity and brilliance of pigmentation of species in this clade is not matched by other micropterigids. The basic melanic wing scales with purple iridescence, so characteristic of the ground colour of micropterigids throughout the world, appear in only a single New Zealand species (*S. ianthina*), the remainder exhibiting a surprising array of colours and patterns. Notable among them is one pattern which occurs in at least six New Caledonian and two New Zealand species where the forewing maculation appears to mimic the head-on view of a salticid spider (Figure 1C, F; see Rota & Wagner 2006, for another lepidopteran example). Note that COI data provide no evidence that this colour pattern is exclusive to a single clade and hence is likely to have evolved repeatedly. Although most species of *Sabatinca* are of typical micropterigid size, it is in this group that the largest species occur, reaching over 6 mm forewing length.

Behaviour. The moths are mainly diurnal except for a number of New Caledonian species, which have been found only in light trap catches. Flight periods vary from those that are annual and active for only a few weeks of the year, to others which are clearly multi-brooded, to others that are biennial. As with most members of the family, adult activity occurs in subdued or dappled sunlight, rarely in full sunshine.

Feeding. All known larvae are foliose liverwort feeders —some evidently with a very restricted host requirement, others apparently polyphagous. From field observations, adult moths rely mainly on fern spores, but are also found on dehiscing lycopod sporangia, or pollen-bearing sedge and angiosperm flowers. One New Caledonian species (sp. 24) has only been found visiting flowers of certain *Zygogynum* (Winteraceae) species, often in company with sp. 11, which also

**FIGURE 1**

Colour images from life of *Sabatinca* species. **A**, *Sabatinca delobeli* Viette, a large (fwl 5.4–6.2 mm) nocturnal species, Riv. Bleue; **B**, *Sabatinca viettei* Minet, a common diurnal species often encountered on fertile *Blechnum* fronds (fwl 3.6–3.9 mm.), Mt Koghis; **C**, *Sabatinca kristenseni* Minet, a diurnal species showing 'salticid' mimic wing maculation (fwl 4.6–5.8 mm), Mt Koghis; **D**, *Sabatinca* sp. 31, Parc des Grandes Fougères; **E**, *Sabatinca heighwayi* Philpott, a species with maximal head and thorax vestiture. (fwl 5.9–6.4 mm), Takaka Hill; **F**, *Sabatinca doroxena* Meyrick, (fwl 3.9–5.1 mm), another species with salticid mimicry maculation, Otaki Forks. A–D. *incongruella* group, New Caledonia; E. *calliarcha* group, New Zealand; F. *chrysargyra* group, New Zealand. Approximately to scale, scale line 1 mm.

occurs on ferns and sedges (Thien *et al.* 1985). If these species are really highly derived within the phylogeny (see Figure 7 below), the association with Winteraceae (a node containing New Caledonian *Zygogynum* has been dated to 47–64 Ma: Marquinez *et al.* 2009) may not be quite the ancient one earlier hypothesized.

Vestiture. Although all micropterigids are characterised by their ‘hairy’ heads, the hairiness on *Sabatinca* species is carried to the extreme. The hair-scale tufts reach their maximum in this lineage, both in length as well as their occurrence over much of the thoracic dorsum. From the pedicel of the antennae, hair-scales can reach to nearly half way along the antennae in some. Hair-scale length can be quantified with reference to the number of antennal flagellomeres covered but is of limited practical taxonomic value due to hair loss in worn specimens. On the thorax, only the anterior region of the mesoscutum is clad with closely fitting lamellar scales. The tegulae, posterior end of mesoscutum and mesoscutellum all bear dense tufts of long erect piliform scales.

Antennae. Strictly moniliform flagellomeres are not present in the *Sabatinca* lineage, but the length of the filiform flagellomeres vary from over three times longer than wide (3.3 l/w in sp. 15) to examples with highly compressed flagellomeres (0.6 l/w in sp. 13), with resulting differences in overall antennal length. The swelling of scape and pedicel reaches a maximum for the family, the scape is indented at mid length and the pedicel is approximately spherical. The presence of a distinct indentation on the scape in three described genera of the ‘southern sabatinoid’ lineage (*Hypomartyria* – Kristensen & Nielsen 1982; *Austromartyria* – Gibbs 2010; *Agrionympha* – Gibbs & Kristensen 2011) is possibly a groundplan synapomorphy of both the ‘southern sabatinoid’ lineage and the *Sabatinca* lineage. The development of antennal colour banding patterns (which greatly facilitate species diagnosis) is a feature of the majority of species.

Wings. In outline, the FW is typically rounded-lanceolate, none are narrow and pointed. The FW outline is modified in species with the salticid mimicry pattern where a broadening of the wing occurs along the tornus-dorsum region, to accommodate several shining silver spots set against a black background, thus emphasising the mimicry of spider eyes. Wings with this pattern are associated with the ‘sessile’ condition of Rs_3 and Rs_4 veins, a configuration so far identified in five species from New Caledonia (including *S. kristenseni* – Figure 1C) and one from New Zealand (*S. doroxena* – Figure 1F). The complete HW R vein is only evident in species of the *calliarcha* group where its basal section is retained (arrow in Figure 2A), a situation that can be interpreted as plesiomorphic. Otherwise, virtually all species of *Sabatinca* carry only a short ‘vestigial spur’, all that remains of R, at about two thirds along Sc_2 (referred to as the ‘recurrent vein’ by Philpott 1923). By no means every New Caledonian micropterigid has been examined for this character, but it may be worth noting that to date only in sp. 10 and sp. 18 is there no trace of the ‘spur’.

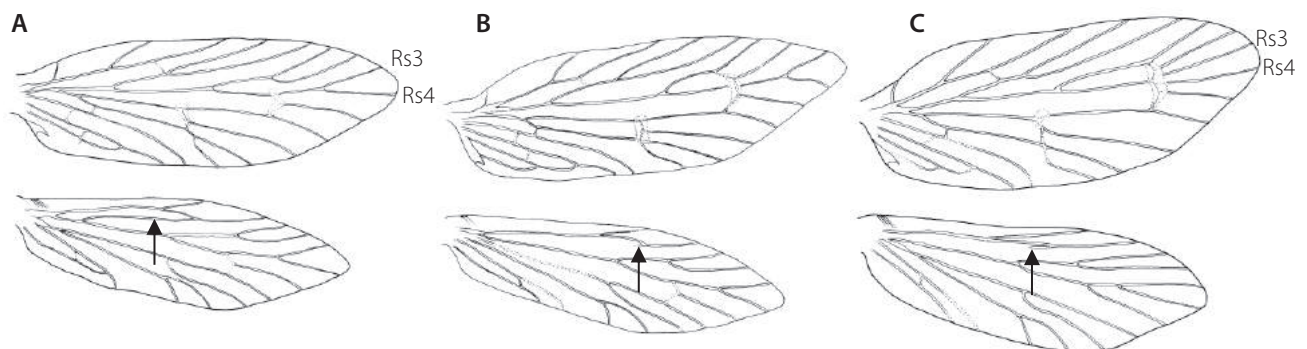


FIGURE 2

Wing venation of *Sabatinca* species. **A**, *Sabatinca calliarcha*; **B**, *Sabatinca incongruella*; **C**, *Sabatinca kristenseni*. Note the full retention of HW vein R in *S. calliarcha*, but its loss, with only a vestigial spur in the other examples (arrows). Also note the sessile FW apical veins, Rs_3 and Rs_4 with broadening of the wing in *S. kristenseni* associated with development of the salticid mimicry pattern.

Abdomen. The S5 gland orifice is consistently 'sabatinoid' in both sexes, meaning raised on a cylindrical protuberance and bearing 2-16 long piliform scales. This form of gland also occurs on all known females of species in the Australian lineage but, apart from *Tasmantrix tasmaniensis*, not on males (see Gibbs 2010). The external gland orifice is absent in two New Caledonian species and one New Zealand species. Male sternite 8 is typically greatly reduced or lost in the Micropterigidae and in *Sabatinca* S8 is never an independent sclerite.

Male genitalia. Dominance of the vinculum (9th segment sclerite) as the most massive component of the male genital apparatus in *Sabatinca* species, is a feature shared with certain other lineages, especially the Asian/North American group but also with isolated examples such as *Hypomartyria*. However, the line of the anteromarginal sulcus is strongly emphasised in *Sabatinca* due to its heavy melanisation. The dorsal region of the vinculum varies greatly between species of *Sabatinca*, in terms of its degree of dorsal closure. The normal form is characterised by a pair of tapering dorsal arms that fail to meet in the mid-line, but ranges from those forming a complete ring with a narrow melanised dorsal 'bridge', to those lacking the dorsal region altogether. The valves are relatively simple, single or double-lobed, sometimes incurved at apex with a small tooth; and often possessing retro-setae on inner surfaces. The simple bilobed or median-lobed form

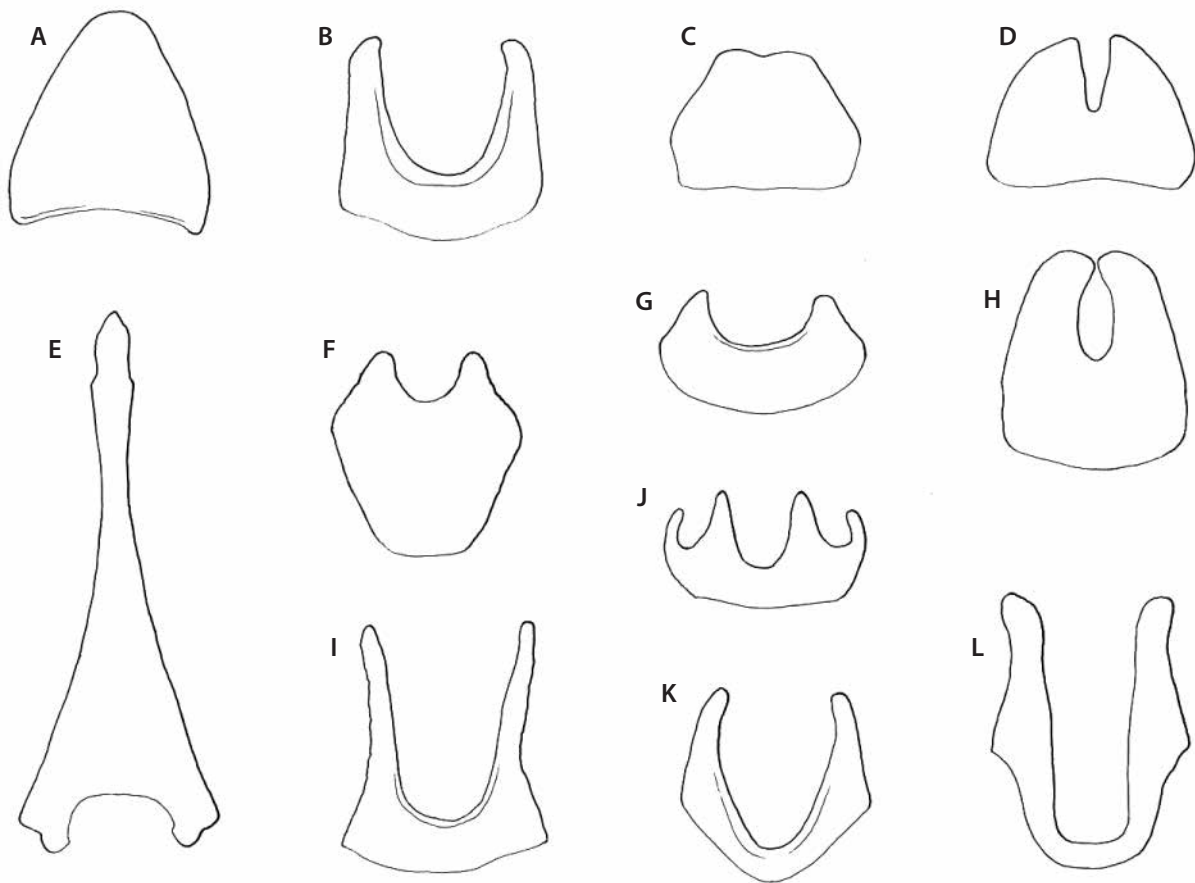


FIGURE 3

Variability in the form of male tergum 10 in species of *Sabatinca*. Dorsal view, only approximately to scale. **A**, *Sabatinca aemula*; **B**, *Sabatinca doroxena*; **C**, *Sabatinca lucilia*; **D**, *Sabatinca incongruella*; **E**, *Sabatinca demissa*; **F**, *Sabatinca* sp. 10; **G**, *Sabatinca* sp. 30; **H**, *Sabatinca* sp. 51; **I**, *Sabatinca* sp. 26; **J**, *Sabatinca* sp. 28; **K**, *Sabatinca viettei*; **L**, *Sabatinca* sp. 21. A-E. New Zealand; F-L. New Caledonia.

of the tergum 10 sclerite is a feature of this lineage but by no means unique to it —indeed regarded as a ground plan plesiomorphy of the family (Kristensen 1984). It is independent, unlike the synscleritous condition of *Micropterix* or undescribed Malagasy taxa (unpublished data), and never divided (as in *Agrionympha* and *Hypomartyria*). Figure 3 shows a range of forms of tergum 10 in *Sabatinca* species. Phallus length varies to greater extremes than in other micropterigids, from short and straight (a widespread micropterigid condition) to considerably longer than the abdomen and thus looped back on itself anteriorly (a unique condition) (Figure 4).

Female genitalia. Specialisation of the Segment 8 pleural region in many *Sabatinca* species is not found in any other micropterigid, but nor does it occur in all *Sabatinca*. An intriguing specialisation occurs in the normally membranous pleural region with the development of a conspicuous sclerotized pouch. Dissection of an intractably locked pair of *Sabatinca* (sp. 50) from New Caledonia has revealed the juxtaposition of the male valve apices with the sclerotised pleural pouches of the female. A correlation between these pouches and the presence of signa within the corpus bursae deserves investigation. Signa, where present, consist of large, tri-radiate sclerotisations (Figure 5C), usually four in number, a condition also found in the Asian/N American lineage (Hashimoto 2006). It has been noted that post-copulation females with large signa frequently also contain many elongate spermatophore fragments within the bursa —possibly broken by the action of the signa themselves. On the other hand, spermatophore residues have never been observed in dissections of females that lack signa. It is likely that some species utilise spermatophores while others have direct sperm transfer, and it can be hypothesised that those utilising a spermatophore may also require a more protracted coupling and thus a more positive locking mechanism.

Larvae. Although superficially similar, in their general ‘sabatinoid’ form, to other liverwort-browsing micropterigid larvae, *Sabatinca* larvae are readily distinguished from those of the Asian/North American lineage (by the position of the abdominal spiracles which lie in the intersegmental grooves in that group but in the middle of the segments in *Sabatinca*) or from other southern sabatinoid larvae (by way of the distinctive chaetotaxy features given in the above diagnosis and Figure 8C, D below).

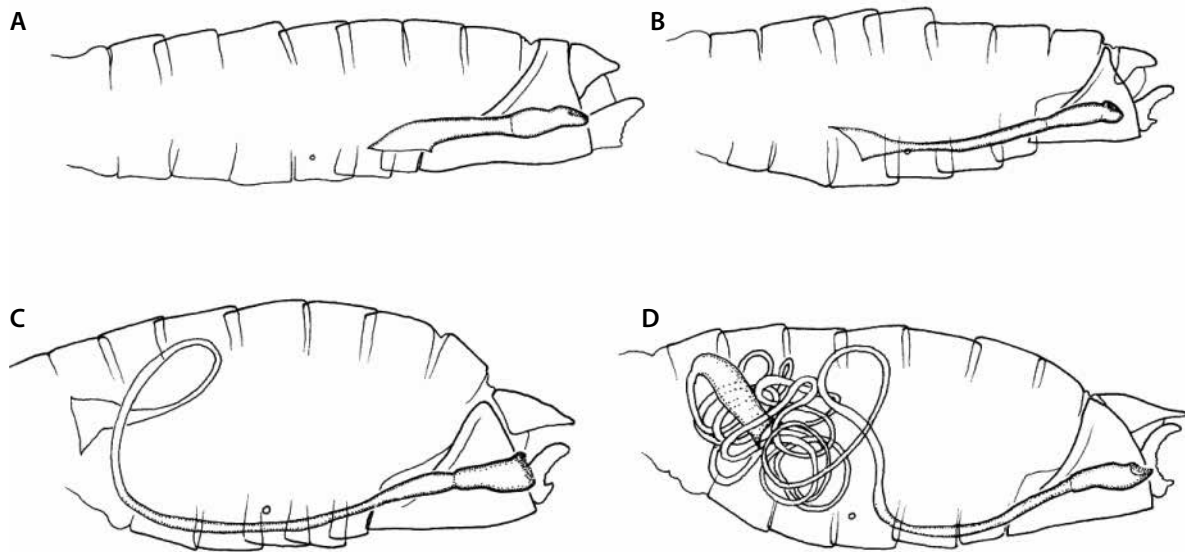
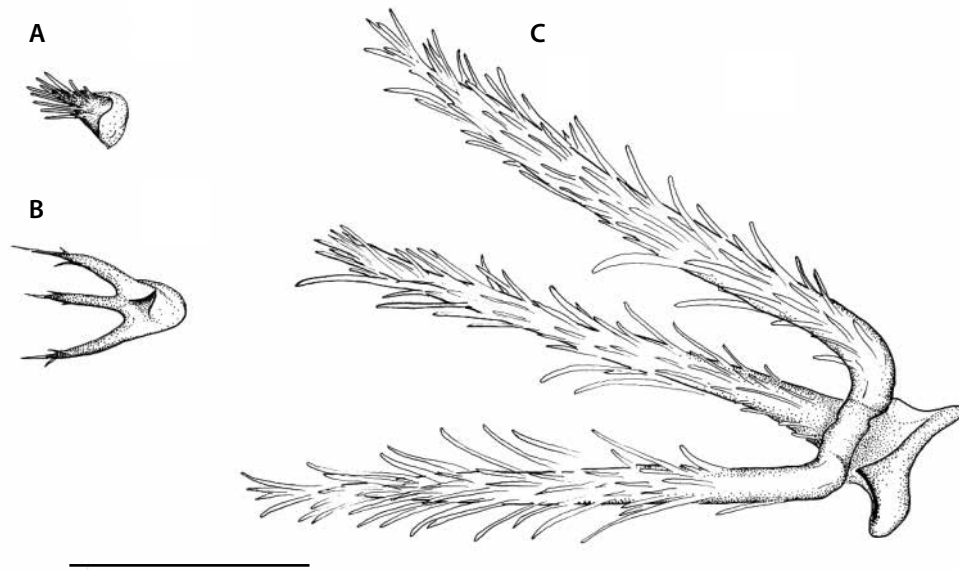


FIGURE 4

Gross morphology of the male phallus in the genus *Sabatinca* showing variability due to elongation of the anterior phallobase. **A**, *Sabatinca incongruella*; **B**, *Sabatinca* sp. 11; **C**, *Sabatinca viette*; **D**, *Sabatinca* sp. 32.

**FIGURE 5**

Morphology of signa in corpus bursae of female *Sabatinca* species. **A**, *Sabatinca demissa*, New Zealand; **B**, *Sabatinca* sp. 30, New Caledonia; **C**, *Sabatinca heighwayi*, New Zealand. Scale line 0.02 mm.

COI barcode. In addition to the unique diagnostic character states mentioned, *Sabatinca* species are the only southern micropterigids with a Methionine rather than Leucine in the 81st complete codon of the COI barcode (representing a first positional A rather than T in the 242nd nucleotide); all the “northern hemisphere” group have the Methionine amino acid state in this position.

SPECIES GROUPS

Sabatinca incongruella group Gibbs & Lees, 2014

INCLUDED SPECIES — *S. incongruella* Walker, 1863, *S. demissa* Philpott, 1923 together with all New Caledonian taxa known to date (*S. delobeli* Viette, 1978, *S. kristenseni* Minet, 1985, *S. viettei* Minet, 1985, and in excess of 50 undescribed taxa).

MORPHOLOGICAL DIAGNOSIS — HW R vein absent but represented by a short spur near middle of Sc2; labial palps 3-segmented (exception: 2-segmented in *demissa*); male tergum 10 undivided, bilobed posteriorly (Figures 3C-L); valves of male genitalia shorter than length of vinculum (usually about 0.3); gonopore without a discrete neck region; female segment 10 elongate, its lateral paired sclerites (papillae) ‘U-shaped’ with length greater than height; spermathecal utriculus with a spherical loculate organ at its distal extremity; corpus bursae usually with four signa, which are normally large & tri-radiate (but exceptions occur). Larva with a single D seta on A8 and either two or three L group macrosetae on T2 and T3 (on lateral fold, just below spiracular line) (see Figure 8C below); the setal form extremely variable from spherical, through short clavate, to thick finger-like, rod-like, to ‘normal’ macrosetae of all lengths from very short to greater than the body diameter.

MOLECULAR DIAGNOSIS — *Sabatinca incongruella* group invariably has an Isoleucine (I) rather than Valine (V) —as in other micropterigids— at the 54th complete codon position, representing a first positional change from G->A. The New Caledonian fauna of the *Sabatinca incongruella* group is further distinct and well supported as monophyletic, by

possessing a Serine (S) rather than Threonine (T) at the 106th complete codon position (representing a first positional change from A->T), and a T rather than I in the 169th complete codon (representing a second positional change from T->C), with a change to Valine in species 29.

DISTRIBUTION — Endemic to New Caledonia and New Zealand.

COMPARATIVE REMARKS — The tendency for *Sabatinca* species to possess highly distinctive patterns of melanic banding along the antennae reaches its peak in this group which, in addition to consistent variation in number of flagellomeres between 16-62, are of high taxonomic value. About 80% of the species exhibit clear-cut black/ochreous patterns of banding (excluding those where melanic intensity is graduated along the length of the antenna). Barcode analysis has indicated that group-specific patterns of antennal banding are supported, implying that these are more than superficial characters.

With about 55 known species currently embraced in this group, it is not surprising that there is considerable variability expressed in their characters, especially of male genitalia which provide the most diagnostic specific characters. Figures 3 and 4 illustrate a sample of the range of morphological diversity within this species group.

In this group the short valves are broadly subdivided into two distal lobes: a dorsal lobe, clasper-like, curving mesally at apex and often with small 'tooth' and/or a patch of retrosetae on its inner surface; and a ventral lobe, usually forming a ventral shelf to the genital atrium. The median plate varies in form but is always a horizontal plate and lacks a lacinate anterior margin. The typically bilobed form of Tergum 10 varies from a shallow notch in a polygonal sclerite (Figure 3D) to a wide 'U-shaped' structure (Figures 3I or 3L), occasionally with the lateral arms curving mesally to meet in the mid-line (Figure 3H). Phallus length variation reaches a maximum in this group; from more or less straight and less than 2x length of S9 (Figure 4A), to up to 20x S9 length and folded back on itself anteriorly (Figure 4C), forming up to 12 coils in one example (Figure 4D). All phallus elongation stems from elongation of the phallobase, which is normally expanded at its anterior end up to 4x its minimum diameter to form a trumpet-shaped bulbus ejaculatorius. Details of gonopore morphology and its surrounding area are valuable for species-level taxonomy but the wider implications of phallic morphology are yet to be investigated in the Micropterigidae.

Modifications to the female pleural region of segment 8 are a feature of this group, but one that is also shared with a few of the *calliarcha* group species. Segment 9 is unspecialised and exhibits varying degrees of ring-formation. The form of the elongate U-shaped terminal papillae on segment 10 appears to be a synapomorphy of this group and the *calliarcha* group, unknown in other micropterigids. Interestingly, the presence of a spherical loculate bulb at the distal end of the spermathecal utriculus, which is shared with the *calliarcha*-group, invites further investigation because a similar, but non-loculate bulb occurs in this position in the genera of the 'southern sabatincoïd' lineage where females are known, e.g. *Austromartyria* (Gibbs 2010), *Agrionympha* (Gibbs & Kristensen 2011), *Squamicornia* (Kristensen & Nielsen 1982). The corpus bursae is extremely variable across this group: from small to very large; normally with four large tri-radiate signa, each consisting of three long melanised arms bearing serrations and stiff bristles, arising from a basal connecting bar which incorporates a hooked process projecting through the bursa wall; signa length varies from 0.07-0.5x overall bursa length (Figure 5).

Larva. A considerable variety of micropterigid larvae have been collected from New Caledonia (largely by GB Monteith, Queensland Museum). Unfortunately, many are unsuitable for DNA extraction, so have not been matched with species of adults. They illustrate a great variety of form and modifications yet to be investigated in detail. Although some types of larvae from New Caledonia will not fit the diagnosis, suffice to say that all known New Caledonian sabatincoïd larvae are of this species group and can be distinguished from New Zealand species by the presence of only a single D seta on T2.

Sabatinca calliarcha group Gibbs & Lees, 2014

INCLUDED SPECIES — *S. calliarcha* Meyrick, 1912, *S. lucilia* Clarke, 1920, *S. heighwayi* Philpott, 1927 and two undescribed taxa from southern New Zealand.

MORPHOLOGICAL DIAGNOSIS — HW R vein is present in its entirety from the basal fork to the point of coalescence with Sc (Figure 2A). Labial palps 3-segmented. Male tegumen 10 strongly bilobed posteriorly with a wide 'U'-shaped emargination (Figure 3C); valves of male genitalia shorter than length of vinculum (0.7-0.9); phallus moderately long (1.6-1.9x seg 9); Gonopore with discrete neck region of smaller diameter than gonopore. Female segment 10 elongate, its lateral papillae sclerites U-shaped with length greater than height (1.6-3.0x); spermathecal utriculus with a spherical loculate organ at its distal extremity; corpus bursae with four large triradiate signa. Larvae with acutely-pointed macrosetae; three L group macrosetae on T2 and two D group setae on A8 (see Figure 8C below).

MOLECULAR DIAGNOSIS — The *calliarcha* group is strongly 'autapomorphic' in its COI barcode compared with all other *Sabatinca*, with a Serine (as in most other micropterigids) rather than an Alanine in the 10th complete codon position (as also in *Zealandopterix/Aureopterix*), a Threonine instead of Alanine in the 73rd position, a Threonine in place of Asparagine in the 104th position, and a Methionine and Proline in place of an Isoleucine and Serine in the 165-166th position, respectively.

Endemic to New Zealand.

COMPARATIVE REMARKS — Although the *calliarcha* group is clearly defined in the COI phylogeny, autapomorphic morphological features are not so evident and involve relatively obscure characters or are those considered plesiomorphic, such as the retention of an entire R vein in the hindwing. Broadly, this group of species closely resemble those of the much larger *incongruella*-group. Thus, apart from the exceptions outlined below, antennal banding patterns are all represented within the variation of the latter group, as is the labial palp segmentation, the male genitalia, and the female genitalia.

The retention of the entire basal portion of hindwing R vein (see Figure 6A below) is unknown in other *Sabatinca* species examined to date but is reported in *Hypomartyria* (Kristensen & Nielsen 1982), *Austromartyria* (Gibbs & Kristensen 2011), and three undescribed Afrotropical genera (NP Kristensen, pers comm) in the 'southern sabatinoid' lineage as defined here. It should be noted that the expression of the basal end of the hindwing R vein can be variable, with *S. lucilia* and an unnamed species from southern South Island exhibiting a condition in which the vein is strong distally but attenuates towards the base. Forewing venation is consistent throughout this group, with distinctly stalked Rs3 and Rs4 in all species.

Features of the male genitalia parallel those in many *incongruella* group species, including the strongly bilobed tergum 10, and the proportions of tergum/valves in relation to segment 9. Minor autoapomorphic features for this group have been identified in the form of the median plate, where the anterior margin is curiously lacinate (smooth in all other *Sabatinca*) and two aspects of the gonopore region of the phallus: the presence of a collar-like neck region supporting the gonopore; and the presence of unique keel-like flanges arising from the ventral bulb.

Sabatinca chrysargyra group Gibbs & Lees, 2014

Note: this report adopts the binomials as listed in Dugdale 1988 except for two New Zealand species which he refers to *Micropardalis* Meyrick 1912 (*aurella*, *doroxena*). A reconsideration of morphological characters and the COI phylogeny clearly show these as members of the *chrysargyra* clade. Meyrick 1912 established the genus *Micropardalis* on the basis of a forewing venational character — Rs4 & 5 veins sessile — a character which is variable, comprises part of a continuum, and is shared with a number of *Sabatinca* species in the *incongruella* group (see Figure 2). We therefore concur with

Kristensen and Nielsen (1979: 140) who proposed the synonymy of *Micropardalis* Meyrick, 1912 with *Sabatinca* Walker, 1863. Molecular data provide further support for this synonymy; the barcodes provide no uniquely shared character changes for *Micropardalis* and the amino acid signature is that of the species-group.

INCLUDED SPECIES — *Sabatinca chrysargyra* (Meyrick, 1885), *S. passalota* (Meyrick 1923), *S. aemula* Philpott, 1924, *S. aurantiaca* Philpott, 1924, *S. aurella* Hudson, 1918, *S. doroxena* (Meyrick, 1888), *S. ianthina* Philpott, 1921, *S. aenea* Hudson, 1923, *S. chalcophanes* (Meyrick, 1885), *S. caustica* Meyrick, 1912, *S. barbarica* Philpott, 1918, *S. quadrijuga* Meyrick, 1912; and two undescribed taxa from South Island, New Zealand.

MORPHOLOGICAL DIAGNOSIS — HW vein R absent but represented by a short spur near middle of Sc₂; labial palps 2-segmented; male tergum 10 undivided, a simple median lobe (Figures 3A & B); valves of male genitalia equal to or longer than vinculum; gonopore without a discrete neck region; female segment 10 sclerite short, never 'U-shaped'; its length:height ratio less than 1; spermathecal utriculus lacking a spherical loculate organ at its distal end; corpus bursae without signa. Larva with two D setae on T₂ and a single L group macroseta on T₂ and T₃ (on lateral fold, just below spiracular line) (see Figure 8D below); the macrosetae short and blunt-tipped, thickened.

MOLECULAR DIAGNOSIS — 35th complete codon of the COI barcode Aspartic acid (D) —as in all other non-*Sabatinca* micropterigids; corresponding 104th (first positional) nucleotide state G. Combination of this character with the diagnostic state for *Sabatinca* clearly defines this species-group.

DISTRIBUTION — Endemic to New Zealand.

COMPARATIVE REMARKS — The 2-segmented labial palps are only found in this group of *Sabatinca* (apart from *S. demissa* cited above). Antennae are moderately long without discrete melanic bands (apart from *S. chalcophanes*) but often becoming gradually more melanic towards the apex. HW vein R normally represented only by a short spur at the point of anastomisation with Sc, or, in rare cases (possibly aberrant forms) occasionally as a distinct vein in its basal section, or totally missing.

The median lobed tergum 10, with a shape ranging from short and shovel-like (Figure 3A) to extremely attenuated (Figure 3B), is the most diagnostic element of this group. Elongate valves, at least as long as vinculum, are another apomorphy of this group and in the female the squarish form of the segment 10 papillae (never U-shaped) is typical of other lineages of Micropterigidae but not of *Sabatinca*. The female segment 8 is never modified in pleural region, but sternite 8 often (five species) and the segment 9 sclerite occasionally (two species) possesses a heavily staining transverse band across the midventral-line, the function of which has not been ascertained. The spermathecal utriculus may be subdivided into two sections but the distal globular loculate section is absent. The corpus bursae lacks signa.

The most frequently encountered micropterigids in the New Zealand fauna, distributed throughout the three main islands.

DISCUSSION

MOLECULAR RESULTS

(Figures 6, 7)

With regard to species delimitation, it suffices to note here that the morphological species designations match very well those circumscribed by DNA barcodes (in almost all cases where multiple exemplars are concerned, with pp >0.95 and usually pp=1). Exceptions occur, where submarginal support possibly indicates a species-complex as in the *S. viettei* group (Figure 6). As evident from Table 1 the cluster number (Barcode Index Number; see www.boldsystems.org).

org/index.php/Public_BarcodeIndexNumber_Home) available on the BOLD database also matches the morphological circumscriptions, except for *Sabatinca* spp. n. 10, 11, 48, *S. ianthina* and *S. chrysargyra* + *S. aemula*. COI currently looks very promising for species delimitation of *Sabatinca* in concert with morphology, and certainly for larva-adult matches (as in the example here of *S. heighwayi*), as well as for sex matches (the identity of females can frequently be doubtful when based on morphology).

In terms of species phylogeny though, even using strong models of evolution, COI barcodes appear of very limited use at current levels of taxon sampling for inferring a robust hypothesis of relationships within *Sabatinca* (few backbone nodes are supported and a similar pattern was found in *Micropterix*: Lees *et al.* 2010b). In any case, a robust hypothesis of *Sabatinca* species relationships seems unlikely to emerge based on the COI barcode marker alone: for example, comparison of Figures 6 and 7 does not mostly reveal an increase in phylogenetic confidence with increased taxon sampling.

By contrast, the barcodes do seem useful for providing a first hypothesis of relationship of clades within *Sabatinca*. Figures 6 and 7 both indicate the same overall topology within *Sabatinca*, with the New Caledonian radiation sharing a most recent common ancestor with a lineage currently occurring in New Zealand. However, only the more densely sampled MrBayes analysis allows a firmly supported inference of a sister relation between the *chrysargyra* group and the *incongruella*-group, and thus a basal position of the *calliarcha* group. In the Beast analysis, this topology remains unresolved.

COI also appears useful for dating of some splits within the Amphiesmenoptera. On the one hand, the dating result shown in Figure 7 seems broadly consistent with diagrams that have recently been presented as a summary of wider molecular and palaeontological data (Figs 13.5, 13.13 in Grimaldi & Engel 2005). On the other hand, it suggests that recent molecular dating of the split of *Apsilochorema* from other Hydrbiobiosidae (Strandberg & Johanson 2010) at around 36 Ma may be too recent, and may therefore be very sensitive to calibration points used, particularly with regard to crown or stem placements for long branches. The dating scheme we present together with the mean rate of COI substitutions across the taxa analysed of 0.00585 per site per Ma (Figure 7), are also consistent with our current knowledge of fossil evidence within Micropterigidae, and with previous molecular dating attempts based on COI only (Lees *et al.* 2010b) or with additional markers (Imada *et al.* 2011), together with a diversification of Japanese endemic genera postdating the isolation of Japan (Imada *et al.* 2011).

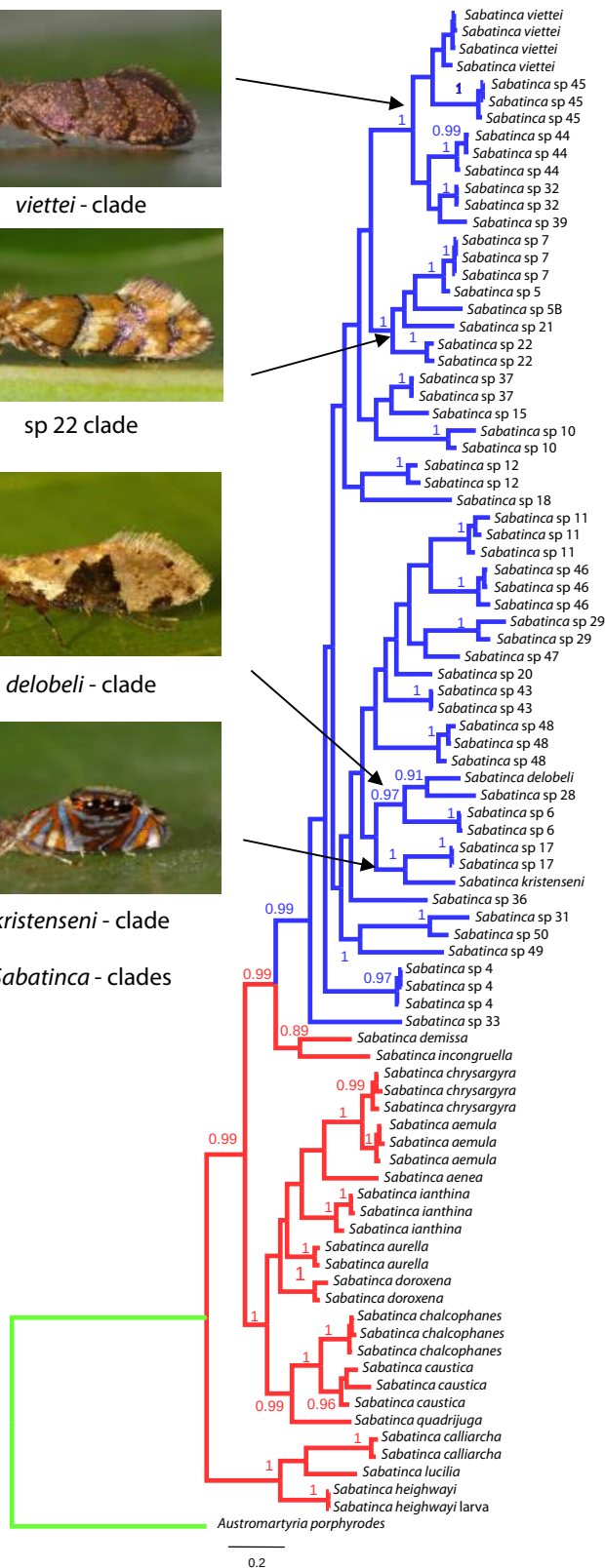
Finally, in terms of overall signal (despite its limitations for probing relationships within *Sabatinca*, and especially the New Caledonian species swarm) perhaps surprisingly, the COI marker does provide consistent and unreversed molecular diagnostics (clearest at amino acid level) for the main morphological clades we recognise. Moreover, it inspires some confidence of the topology at deeper levels concerning the generic relationships of other Micropterigidae, for example for the relationships of *Aureopterix*, *Zealandopterix* and *Tasmantrix* (Figure 7), when considered against existing knowledge of their morphology (Gibbs 2010), and therefore also for our dating results. However, such topologies and even evidence of a primary southern-northern hemisphere dichotomy within the family clearly remain to be tested with additional molecular markers (e.g. Imada *et al.* 2011). In any case, a position of *Sabatinca* that is internal to northern hemisphere lineages (Bayesian support in Fig. 2 of Imada *et al.* 2011; from this study, we confirm the single sequence identity as “*viettei*”: Figure 6) seems to us to be clearly an artefact of limited taxon sampling.

FIGURE 6

Phylogeny of a large sample of *Sabatinca*, rooted using *Austromartyria*, based on a partitioned (1st + 2nd) + 3rd-position analysis of COI barcodes using MrBayes 3.1. Support levels are shown as posterior probability (pp) support, where at least 90% (those over 94% are here considered reliable). Blue: New Caledonia. Red: New Zealand. Green: Australia. Three main clades within the genus supported at present (pp>0.95) are the *chrysargyra* group- New Zealand (and within that a sub-clade including *S. quadrijuga* and *S. chalcophanes*); the *calliarcha* group- New Zealand; and the *incongruella* group- New Zealand and New Caledonia. At least four New Caledonian *Sabatinca* sub-clades are also supported, in particular (pp=1; Figures 6, 7): a “*viettei*”-clade, a “sp. 22”-clade, a “*kristenseni*”-clade and a “*delobeli*”-clade.

*viettei* - clade

sp 22 clade

*delobeli* - clade*kristenseni* - clade*Sabatinca* - clades

MICOW384-10
MICOW433-10
AB608899
MICOW120-09
MICOW419-10
MICOW457-10
MICOW458-10
MICOW121-09
MICOW141-09
MICOW435-10
MICOW133-09
MICOW412-10
MICOW044-09
MICOW416-10
MICOW147-09
MICOW393-10
MICOW113-09
MICOW431-10
MICOW129-09
MICOW130-09
MICOW131-09
MICOW136-09
MICOW048-09
MICOW122-09
MICOW116-09
MICOW408-10
MICOW432-10
MICOW119-09
MICOW126-09
MICOW117-09
MICOW118-09
MICOW397-10
MICOW094-09
MICOW095-09
MICOW049-09
MICOW132-09
MICOW392-10
MICOW138-09
MICOW400-10
MICOW139-09
MICOW150-09
MICOW418-10
MICOW144-09
MICOW404-10
MICOW042-09
MICOW401-10
MICOW114-09
MICOW402-10
MICOW417-10
MICOW125-09
MICOW436-10
MICOW135-09
MICOW043-09
MICOW146-09
MICOW145-09
MICOW403-10
MICOW407-10
MICOW406-10
MICOW134-09
MICOW037-09
MICOW036-09
MICOW009-09
MICOW008-09
MICOW429-10
MICOW001-09
MICOW004-09
MICOW002-09
MICOW018-09
MICOW014-09
MICOW015-09
MICOW013-09
MICOW011-09
MICOW010-09
MICOW016-09
MICOW017-09
MICOW021-09
MICOW022-09
MICOW023-09
MICOW019-09
MICOW030-09
MICOW020-09
MICOW026-09
MICOW040-09
MICOW039-09
MICOW038-09
MICOW101-09
MICOW460-10
MICOW282-10



sp 15



sp 10



sp 11



sp 48

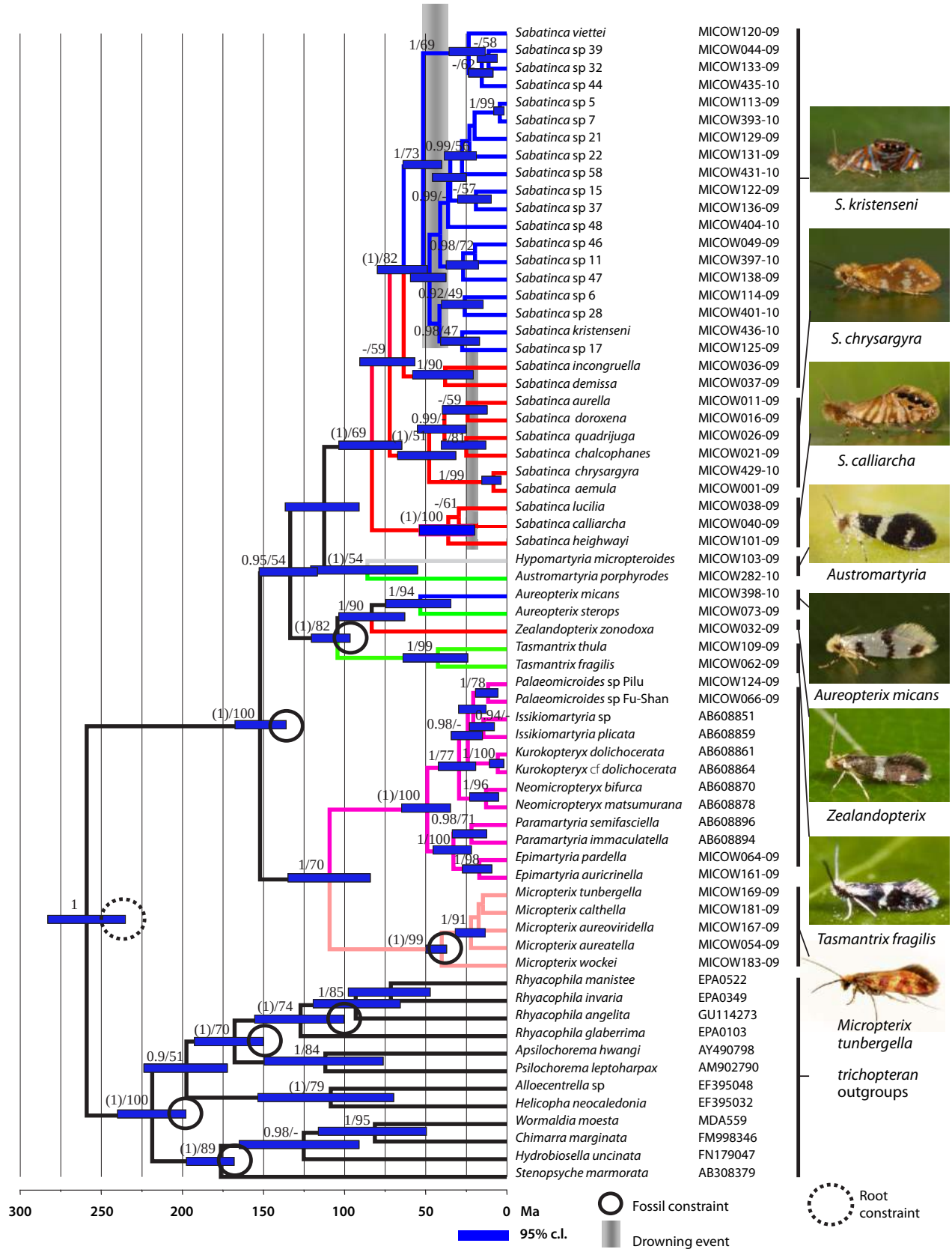


sp 6



sp 33

*S. incongruella**S. chrysargyra**S. ianthina**S. calliarcha*



BIOGEOGRAPHIC DISCUSSION

Although a revised taxonomy and preliminary phylogeny of Micropterigidae and *Sabatinca* clades are the practical outcomes of this systematic research, it is the biogeographic implications which are particularly relevant in light of the current debate on the age and source of New Caledonia's endemic terrestrial biota or, for that matter, New Zealand's as well. This debate centres around the history of isolated islands on the largely submerged continent of Zealandia. Tasman Sea spreading (85–55 Ma) initially separated Zealandia from eastern Gondwana (Mortimer *et al.* 2006) but the configuration of land areas and the nature of its terrestrial life is largely unknown apart from fragments pieced together from the fossil record of New Zealand. Since the 1970's a number of biologists have claimed that relictual biota from Cretaceous times still survives on both New Caledonia and New Zealand (e.g. Morat 1993, Lowry 1998, Gibbs 2006, Giribet & Boyer 2010), most famously for the kagu which has been recovered as sister to the sunbittern from South America (Fain & Houde 2004) and *Amborella trichopoda* often considered to be the extant sister of all angiosperms (Soltis & Soltis 2004). However, an ever-increasing number of studies, especially using molecular phylogenetics, provide evidence to the contrary in which much more recent establishment dates are being supported, in agreement with the estimated geological ages of the modern islands (see Séret 2007, and review of case studies in Wallis & Trewick 2009 and Cruaud *et al.* 2012).

'Drowning events' in the history of New Caledonia and New Zealand follow very different geological pathways and timing, but of course, any submergence will eliminate relictual terrestrial biota unless it is able to persist on adjacent land. In New Caledonia, evidence for total submergence is strong with marine sedimentary rocks formed under high pressure indicating the region was in deep water for about 20 Ma during the Palaeocene and Eocene (Aitchison *et al.* 1998; Paris 1981). This was followed by ophiolitic obduction in the Eocene caused by collision between the Loyalty Arc and Australian plate around 45 Ma, resulting in a 2 km thick layer of oceanic crust being placed over the still submerged continental crust (Schellert *et al.* 2006). There is a possibility of other islands existing on the Loyalty or Norfolk ridges at this time (Paris 1981), but not providing any direct continuity between Gondwana and the modern island (Meffre *et al.* 2006). Modern New Caledonia re-emerged from the sea in the late Eocene/early Oligocene, at about 37 Ma (Schellert *et al.* 2006).

While the above events were occurring, 1500 km to the SSE the future New Zealand region, long after (>50 Ma) its separation from Gondwana, was steadily eroding and sinking to become a low-lying archipelago of islands of uncertain area, with estimates varying from about 18% of the present land area (Cooper & Cooper 1995) to complete submergence at 23 Ma (Campbell & Hutching 2007). Although retention of minimal land represents a widely accepted geological view, the notion that the 'Oligocene drowning' was total has been taken up enthusiastically by a number of molecular biologists whose researches indicate establishment and radiation dates for modern New Zealand lineages of less than 20 Ma — *i.e.* after the maximum marine transgression. Thus two very different drowning scenarios on the Zealandia plate are generating similar debates about the sources and colonisation timing of modern lineages on New Caledonia and New Zealand. The micropterigid data presented here is of particular significance since it provides a direct challenge to both 'drowning' scenarios.

We have already outlined why we consider these diminutive forest moths to be ideal candidates for deep-time biogeographic studies. To that can be added the notion of short-range endemism (Harvey 2002; Giribet & Boyer 2010) which is especially applicable to the cryptic invertebrates of permanently moist micro-habitats. Despite being fully winged,

FIGURE 7

Dating analysis of reduced set of 66 terminals including 12 trichopteran outgroups and representatives of all five clades currently considered within the Micropterigidae. Fossil constraints indicated by circles at nodes; scale bar in millions of years. Bars represent mean and 95% confidence limits for all nodes supported by a posterior probability >50%. Values at nodes indicate posterior probability support level. Biogeographic colouring as in Figure 6. plus: Purple: SE Asia; Pink: Europe; Grey: South America. Trichoptera not colour coded. Note that the derived New Caledonian *Sabatinca* diversification began *ca.* 52 Ma (95% cls. 40, 64), that of the *incongruella* group *ca.* 64 Ma (48.9, 79.7) and that of the genus *Sabatinca* *ca.* 84 Ma (64.7, 103.5), that of *chrysargyra* group *ca.* 48.7 Ma (31.3, 67.2), and that of *calliarcha* group *ca.* 36.9 Ma (21.9, 53.1). Similarly of relevance, the Australia-New Caledonia split in *Aureopterix* is *ca.* 53.5 Ma (34.5, 74.5) and the *Zealandopterix*-*Aureopterix* split *ca.* 83.2 Ma (62.9, 103.5). The mean rate of COI substitutions across the taxa analysed was 0.00585 per site per Ma (95% cls 0.00412, 0.00793).

the restricted geographic patterns of the majority of New Caledonian micropterigids stands as evidence for their lack of active dispersal mechanisms (Imada *et al.* 2011 reach similar conclusions for Japanese micropterigids). Moreover, the world distribution pattern of Micropterigidae also displays an absence of any clear cases of long-distance dispersal (*e.g.* to recent volcanic islands separated by deep seas). These attributes have been exploited here with a resolved taxon-rich phylogeny and fossil-calibrated molecular dating analysis.

From a series of eight papers on the origin and diversification of the New Caledonian biota (presented at the VI Southern Connection Congress, Bariloche, Argentina, Feb 2010) the overwhelming conclusion was summed up by the statement that ‘cumulative phylogenetics studies identify more and more groups in New Caledonia that are 35 Ma or younger, often with Australia as a source area’ (Munzinger 2010). While that may well represent the majority view from studies conducted so far, it should be cautiously noted that biogeography is not solely concerned with majority patterns. Indeed, Joseph Hooker, regarded as the ‘real founder of causal historical biogeography’ (Brundin 1988), once commented that ‘by a single plant the floras of Chile and New Zealand are connected’ thus emphasising the importance of explaining the ‘exceptions’ as well as majority patterns (Hooker 1853). Our present understanding of the phylogeny of Micropterigidae clearly supports two sources for the fauna of New Caledonia —either from the Australian continent (as is most likely in the case of the two described Australian group species); or from New Zealand (as is the case for the majority *Sabatinca* taxa discussed here). In the course of Zealandian history, the Australian-derived lineage also reached New Zealand, but the New Zealand-derived *Sabatinca* lineage apparently failed to colonise Australia. It could, of course,

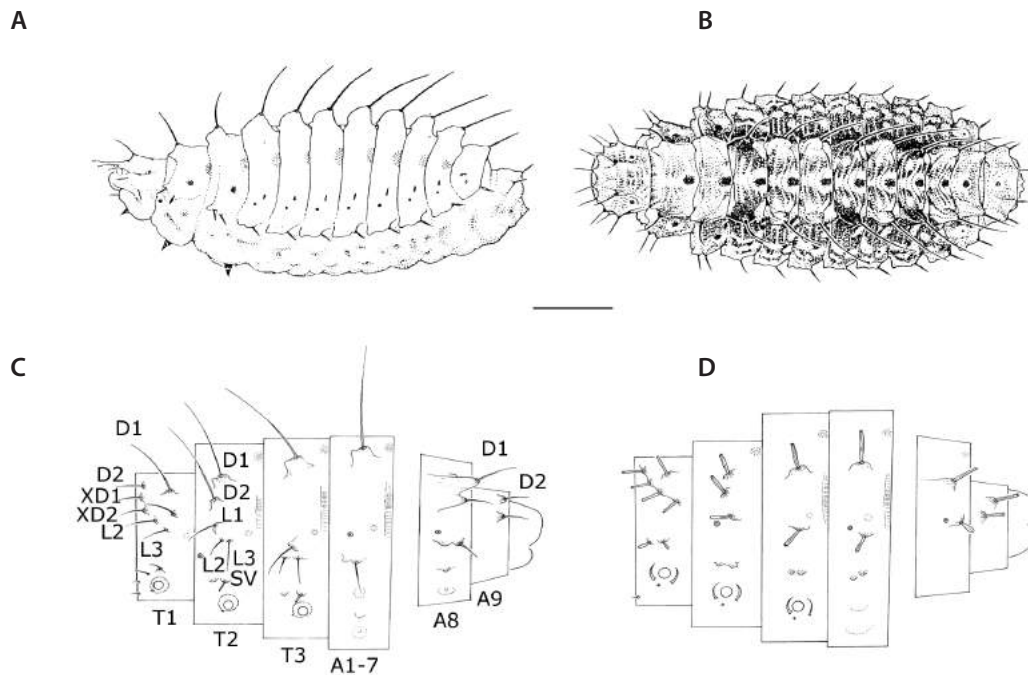


FIGURE 8

Larval morphology. **A**, *Sabatinca kristenseni* mature larva, lateral view; **B**, *S. kristenseni* larva, dorsal view, showing pigmentation; dorsal ridges marked by rows of D1 macrosetae. Note the dark median spots represent muscle attachment points; **C**, *Sabatinca calliaracha*, chaetotaxy of thoracic and abdominal segments; **D**, *Sabatinca chalcophanes*, chaetotaxy of thoracic and abdominal segments. Scale line 1 mm. Drawings A and B by Des Helmore, Landcare Research, Auckland, New Zealand, with permission.

have become extinct there; while the sister group of *Sabatinca* is as yet uncertain, our dating analysis (Figure 7) suggests it represents an old micropterigid lineage sister to the “southern sabatinoid” clade and probably predating the separation of Australis and Zealandia). This dating analysis supports a vicariant explanation for the occurrence of both lineages in New Zealand (84 Ma) and also challenges the age of colonisation of New Caledonia by suggesting that the derived New Caledonian radiation of *Sabatinca incongruella* group could have colonised the island at *ca* 64 Ma and begun diversifying at *ca*. 52 Ma. The dates recovered from this analysis further imply the existence of land somewhere in the region prior to the upthrust of New Caledonia.

The *Sabatinca* lineage is shown to have existed for considerably longer in the New Zealand region than in New Caledonia. According to our micropterigid calibration, the genus *Sabatinca* started diversifying around 84 Ma; the *incongruella* group began around 64 Ma, and *chrysargyra* group apparently started radiating by *ca*. 49 Ma (Figure 7). These dates are well before the timing of the New Zealand drowning hypothesis —*ca*.25–22 Ma (Gibbs 2006), thus challenging its impact as an overall extinction event.

The Australia–New Caledonia split in *Aureopterix*, which we date at *ca*. 53.5 Ma, is intriguing as it seems rather too late for a vicariance explanation, although the *Zealandopterix*–*Aureopterix* split at *ca*. 83 Ma is consistent with one. The analysis implies that *Aureopterix micans* could represent relic of a event to New Caledonia across the Coral Sea. *Nannopterix* (Gibbs 2010), not barcoded here, also needs to be taken into account to complete this picture.

The conclusion presented here contradicts the consensus reached at the VI Southern Connections meeting. Is it alone in implying that either the island is older than has been predicted from its geology, or, was there an adjacent forested island that is now submerged? Indeed, another phylogenetic study of a group of cryptic invertebrates has presented similar results. The New Caledonian endemic harvestman family Troglosironidae likewise indicates an ancient lineage with subsequent diversification of the crown group on the island prior to the Oligocene (Sharma & Giribet 2010). In this example the sister groups are from Northern South America and Africa. Both examples highlight the complex nature of New Caledonia's biota, its sources and its timing. It is probably no coincidence that similar research on the New Zealand biota is also revealing a mix of lineages: a few of which appear to be ancient, predating the Oligocene ‘drowning’ event (*e.g.* Tennyson *et al.* 2010); together with a majority of post-Oligocene colonisers (*e.g.* Goldberg *et al.* 2008, Wallis & Trewick *et al.* 2009). Phylogenetic research on a wide range of organisms indicates that both the archaic and the more recently arrived groups have undergone major radiations during Miocene or post-Miocene times (*e.g.* Allwood *et al.* 2009; Bunce *et al.* 2009; Wallis & Trewick 2009). Although there is general agreement over the initial isolation of Zealandia from the eastern margin of Australis, 80–55 Ma, the subsequent histories of New Caledonia and New Zealand as emergent land are more uncertain. Did some land persist somewhere nearby throughout the marine inundation scenarios? Where was it? What can the biota tell us? Schellart *et al.* (2009) have reopened the geological debate by the discovery of a subducted tectonic plate between New Caledonia and New Zealand, thereby revealing the possibility of a geographical connection between proto-New Caledonia and proto-New Zealand somewhere between 50 and 20 million years ago, possibly through a long chain of volcanic islands. It seems that the ‘classical’ view of two SW Pacific Gondwanan island refuges where archaic groups have survived for 80 Ma should now be discarded, but more intensive studies of a wider array of New Caledonia and New Zealand fauna are required before an acceptable ‘catch phrase’ is found to replace it.

Other phylogenies that have recovered various sister group relationships between New Zealand and New Caledonia include *Metrosideros* (Wright *et al.* 2000); *Corynocarpus* (Wagstaff & Dawson 2000); the stick insect clade *Lanceocercata* (Buckley *et al.* 2010); moss bugs (Peloriidiidae) (Burckhardt 2009); cicadas (Tibicinidae) (Arensburger *et al.* 2004); wetas (Anostostomatidae) (Pratt *et al.* 2008); Geckonidae (Nielsen *et al.* 2011) and Scincidae (Chappell *et al.* 2009). Which way did this terrestrial traffic move? These studies offer both northward and southward interpretations. As many before us have stated, New Zealand is one of the most challenging places on earth to explain. We should now extend that phrase to include the other major terrestrial fragment of Zealandia —New Caledonia. Zealandian biogeography is poised to become a focal point of world interest as more studies shed light on this fascinating region. It is time to move beyond the fashionable drowning scenarios of today and attempt to understand the history of former land on the continent of Zealandia. ‘The map of this day keeps the records, the maps of the past rationally account for them.’ (Croizat 1964: 85).

ACKNOWLEDGMENTS

We are particularly grateful to Christian Mille, Pocquereux Fruit Research Station, La Foa, for hospitality and assistance while on field trips to New Caledonia. David Paulaud, DDE, Prov Sud, and Jean-Jerome Cassan, DDE, Prov Nord, provided the necessary permits for collecting in New Caledonia and Department of Conservation has willingly done the same for New Zealand. New Caledonian specimens have generously been made available for this study from Don Davis, Smithsonian Institution; Kjell-Arne Johanson, Swedish Museum of Natural History; and Geoff Monteith, Queensland Museum. Invaluable advice was received from Niels P Kristensen during the preparation of this paper. Joël Minet is thanked for his assistance with the French abstract. DCL was assisted by a STUDIUM fellowship and funded by INRA and ERC EMARES #250325 during the preparation of this manuscript. Rodolphe Rougerie is thanked for his dedicated assistance with the Micropterigidae barcoding project at University of Guelph, partly funded by Genome Canada. Atsushi Kawakita generously made available sequence data underlying the work of Imada *et al.* 2011 in advance of its release.

REFERENCES

- AITCHISON J.C., IRELAND T.R., CLARKE G.L., CLUZEL D., DAVIS A.M. & MEFFRE S. 1998 — Regional implications of U/Pb SHRIMP age constraints on the tectonic evolution of New Caledonia. *Tectonophysics* 299: 333-343.
- ALLWOOD J., GLEESON D., MAYER G., DANIELS S., BEGGS J.R. & BUCKLEY T.R. 2009 — Support for vicariant origins of the New Zealand Onychophora. *Journal of Biogeography* 37: 669-681.
- ANSORGE J. 2003 — Upper Liassic Amphiesmenopterans (Trichoptera + Lepidoptera) from Germany. *Acta zoologica cracoviensia* 46 (suppl.): 285-290.
- ARENSBURGER P., BUCKLEY T.R., SIMON C., MOULDS M. & HOLSINGER K.E. 2004 — Biogeography and phylogeny of the New Zealand cicada genera (Hemiptera: Cicadidae) based on nuclear and mitochondrial DNA data. *Journal of Biogeography* 31: 557-569.
- AZAR D., NEL A. & GÈZE R. 2002 — Use of Lebanese amber inclusions in paleoenvironmental reconstruction, dating and paleobiogeography. *Acta zoologica cracoviensia* 46 (suppl.): 393-398.
- BOTOSANEANU L. & WICHARD W. 1983 — Upper Cretaceous Siberian and Canadian amber caddisflies (Insecta: Trichoptera). *Bijdragen tot de Dierkunde* 53: 187-217.
- BRUNDIN L.Z. 1988 — Phylogenetic biogeography. Chapter 11, in MYERS A.A. & GILLER P.S. (eds), *Analytical Biogeography*. London, Chapman & Hall: 343-369.
- BUCKLEY T.R., ATTANAYAKE D., NYLANDE J.A.A. & BRADLER S. 2010 — The phylogenetic and biogeographical origins of the New Zealand stick insects (Phasmatodea). *Systematic Entomology* 35: 207-225.
- BUNCE M., WORTHY T.H., PHILLIPS M.J., HOLDAWAY R.N., WILLERSLEV E., HAILE J., SHAPIRO B., SCOFIELD R.P., DRUMMOND A., KAMP P.J.J. & COOPER A. 2009 — The evolutionary history of the extinct ratite moa and New Zealand Neogene palaeogeography. *Proceedings of the National Academy of Sciences of the United States of America* 106: 20646-20651.
- BURCKHARDT D. 2009 — Taxonomy and phylogeny of the Gondwanan moss bugs or Peloridiidae (Hemiptera, Coleorrhyncha). *Deutsche Entomologische Zeitschrift* 56: 173-235.
- CAMPBELL H. & HUTCHING G. 2007 — In search of ancient New Zealand. Penguin Books, North Shore, New Zealand, 239 p.
- CARTER D.J. & DUGDALE J.S. 1982 — Notes on collecting and rearing *Micropterix* (Lepidoptera: Micropterigidae) larvae in England. *Entomologists' Gazette* 33: 43-47.
- COOPER A. & COOPER R.A. 1995 — The Oligocene bottleneck and New Zealand biota – Genetic record of a past environmental crisis. *Proceedings of the Royal Society of London. B* 261: 293-302.
- CHAPPELL D.G., RITCHIE P.A. & DAUGHERTY C.H. 2009 — Origin, diversification, and systematics of the New Zealand skink fauna (Reptilia: Scincidae). *Molecular Phylogenetics and Evolution* 52: 470-487.
- CRUAUD A., JABBOUR-ZAHAB R., GENSON G., UNGRICHT S. & RASPLUS J.-Y. 2012 — Testing the emergence of New Caledonia: fig wasp mutualism as a case study and a review of evidence. *PloS ONE* 7:e30941.
- CROIZAT L. 1964 — Space, time, form: the biological synthesis. Published by the author. Caracas, 881 p.
- DAVIS D.R. & LANDRY J.-F. 2012 — A review of the North American genus *Epimartyria* (Lepidoptera, Micropterigidae) with a discussion of the larval plastron. *Zookeys* 2012: 37-83.
- DELCLÒS X., ARILLO A., PEÑALVER E., BARRÓN E., SORIANO C., LÓPEZ DEL VALLE R., BERNÁRDEZ E., CORRAL C. & ORTUÑO V.M. 2007 — Fossiliferous amber deposits from the Cretaceous (Albian) of Spain. *Comptes Rendus Palevol* 6: 135-149.
- DRUMMOND A.J. & RAMBAUT A. 2007 — BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7: 214.
- DUGDALE J.S. 1988 — Lepidoptera – annotated catalogue, and keys to family group taxa. Fauna of New Zealand 14, 262 p.
- FAIN M.G. & HOUE P. 2004 — Parallel radiations in the primary clades of birds. *Evolution*, 58: 2558-2573.
- GIBBS G.W. 1983 — Evolution of the Micropterigidae in the SW Pacific. *Geojournal* 7: 505-510.
- GIBBS G.W. 2006 — Ghosts of Gondwana: the history of life in New Zealand. Craig Potton Publishing, 432 p.
- GIBBS G.W. 2010 — Micropterigidae (Lepidoptera) of SW Pacific: a revision with the establishment of five new genera from Australia, New Caledonia and New Zealand. *Zootaxa*, 2520: 1-48.
- GIBBS G.W. & KRISTENSEN N.P. 2011 — *Agrionympha*, the long-known South African jaw-moths: a revision with descriptions of new species (Lepidoptera, Micropterigidae). *Zootaxa*, 2764: 1-21.
- GIBBS G.W., KOBAYASHI Y., SUZUKI H., HASHIMOTO S., LEES D.C., SUGIMOTO M. & SAIGUSA T. 2004 — Molecular phylogeny of Micropterigidae.

- Proceedings of XXII International Congress of Entomology. 2004, Brisbane, Australia. Abstract only.
- GIRIBET G. & BOYER S.L. 2010 — 'Moa's Ark' or 'Goodbye Gondwana': is the origin of New Zealand's terrestrial invertebrate fauna ancient, recent, or both? *Invertebrate Systematics* 24: 1-8.
- GOLDBERG J., TREWICK S.A. & PATERSON A.M. 2008 — Evolution of New Zealand's terrestrial fauna: a review of molecular evidence. *Philosophical Transactions of the Royal Society B, Biological Sciences* 363: 3319-3334.
- GRANDCOLAS P., MURIENNE J., ROBILLARD T., DESUTTER-GRANDCOLAS L., JOURDAN H., GUILBERT E. & DEHARVENG L. 2008 — New Caledonia: a very old Darwinian island? *Philosophical Transactions of the Royal Society B* 363: 3309-3317.
- GRIMALDI D.A., ENGEL M.S. & NASCIMBENE P.C. 2002 — Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates* 3361: 1-72.
- GRIMALDI D. & ENGEL M.S. 2005 — Evolution of the insects. Cambridge University Press, Cambridge xv + 55 p.
- HALL T.A. 1999 — BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95-98.
- HARVEY Z. 2002 — Short-range endemism among the Australian fauna: some examples from non-marine environments. *Invertebrate Systematics* 16: 555-570.
- HASHIMOTO S. 2006 — A taxonomic study of the family Micropterigidae (Lepidoptera, Micropterigoidea) of Japan, with the phylogenetic relationships among the Northern Hemisphere genera. *Bulletin of the Kitakyushu Museum of Natural History and Human History, A (Natural History)* 4: 39-109.
- HEADS M. 2008 — Panbiogeography of New Caledonia, south west Pacific: basal angiosperms on basement terranes, ultramafic endemics inherited from volcanic island arcs and old taxa endemic to young islands. *Journal of Biogeography* 35: 2153-2175.
- HIROWATARI T., HASHIMOTO S., JINBO U. & WANG M. 2009 — Descriptions of two new species of *Vietomartyria* Hashimoto & Mey (Lepidoptera, Micropterigidae) from South China, with reference to autapomorphies of the genus. *Entomological Science* 12: 67-73.
- HOLLOWAY J.D. 1979 — A survey of the Lepidoptera, Biogeography and Ecology of New Caledonia. The Hague, Dr W. Junk.
- HOOKE J.D. 1853 — Introductory Essay, Flora Novae-Zelandiae. The botany of the Antarctic Voyage of H. M. Discovery ships Erebus and Terror in the years 1839-1843. London, Lovell Reeve.
- IMADA Y., KAWAKITA A. & KATO M. 2011 — Allopatric distribution and diversification without niche shift in a bryophyte-feeding basal moth lineage (Lepidoptera: Micropterigidae). *Proceedings of the Royal Society B* 278: 3026-3033.
- IVANOV B.D. & SUKATSCHEVA I.D. 2002 — Order Trichoptera Kirby, 1813. The caddisflies, in QUICK D. & RASNITSYN A.P. (eds), The History of Insects, Kluwer Publ., Dordrecht, Boston, London: 199-220.
- KRISTENSEN N.P. 1984 — Skeleto-muscular anatomy of the male genitalia of *Epimartyria* (Lepidoptera: Micropterigidae). *Entomologica Scandinavica* 15: 97-112.
- KRISTENSEN N.P. & NIELSEN E.S. 1979 — A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). *Steenstrupia* 5: 69-147.
- KRISTENSEN N.P., SCOBLE M.J. & KARSHOLT O. 2007 — Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. *Zootaxa* 1668: 699-747.
- LEES D.C., ROUGERIE R., ZELLER-LUKASHORT C. & GIBBS G.W. 2010a — Barcoding the base of Lepidoptera: exploring global diversity and evolution of the Micropterigidae. [Abstract S206]. 2nd Symposium on the European Consortium for the Barcode of Life, Braga, 02-04 June 2010.
- LEES D.C., ROUGERIE R., ZELLER-LUKASHORT H.C. & KRISTENSEN N.P. 2010b — DNA mini-barcodes in taxonomic assignment: a morphologically unique new homoneurous moth clade from the Indian Himalayas described in *Micropterix* (Lepidoptera, Micropterigidae). *Zoologica Scripta* 39: 642-661.
- LOWRY P.P. 1998 — Diversity, endemism, and extinction in the flora of New Caledonia: a review, in PENG C.I. & LOWRY P.P. (eds), Proceedings of the International Symposium on Rare, Threatened, and Endangered Floras of Asia and the Pacific. Academia Sinica, Monogr. Ser. no. 16. Institute of Botany, Taipei, Taiwan: 181-206.
- MARQUÍNEZ X., LOHMANN L.G., SALATINO M.L.F., SALATINO A. & GONZÁLEZ F. 2009 — Generic relationships and dating of lineages in Winteraceae based on nuclear (ITS) and plastid (rps16 and psbA-trnH) sequence data. *Molecular Phylogenetics and Evolution* 53: 435-449.
- MEFFRE S., CRAWFORD A.J. & QUILTY P.G. 2006 — Arc continent collision forming a large island between New Caledonia and New Zealand in the Oligocene. Australian Earth Sciences Convention, AESC, Melbourne: 1-3.
- MEY W. 2011 — On the systematic position of *Baltimartyria* Skalski, 1995 and description of a new species from Baltic amber (Insecta, Lepidoptera, Micropterigidae). *Zookeys* 130: 331-342.
- MCKENNA D.D. & FARRELL B.D. 2006 — Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proceedings of the National Academy of Sciences of the United States of America* 103: 10947-10951.
- MINET J. 1985 — Description de nouveaux *Sabatinka* néo-calédoniens et redéfinition du genre en fonction de considérations phylogénétiques (Lepidoptera, Micropterigidae). *Nouvelle Revue d'Entomologie* 2: 285-297.
- MORAT P. 1993 — The terrestrial biota of New Caledonia. *Biodiversity Letters* 1: 69-70.
- MORTIMER N. 2004 — New Zealand's geological foundations. *Gondwana Research* 7: 261-272.
- MORTIMER N., HOERNLE K., HAUFF F., PALIN J.M., DUNLAP W.J., WERNER R. & FAURE K. 2006 — New constraints on the age and evolution of the Wishbone Ridge, southwest Pacific Cretaceous microplates, and Zealandia-West Antarctica breakup. *Geology* 34: 185-189.
- MUNZINGER J. 2010 — Origin of the flora of New Caledonia, past and present knowledge. Abstract only: VI Southern Connection Congress, Bariloche.
- MURIENNE J. 2009 — Testing biodiversity hypotheses in New Caledonia using phylogenetics. *Journal of Biogeography* 36: 1433-1434.
- MURIENNE J., GRANDCOLAS P., PIULACHS M.D., BELLES X., D'HAES C., LEGENDRE F., PELLENS R. & GUILBERT É. 2005 — Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? *Cladistics* 21: 2-7.
- NIELSEN S.V., BAUER A.M., JACKMAN T.R., HITCHMOUGH R.A. & DAUGHERTY C.D. 2011 — New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. *Molecular Phylogenetics and Evolution* 59: 1-22.
- PARIS J.P. 1981 — Géologie de la Nouvelle-Calédonie. *Mémoires du Bureau de Recherches Géologiques et Minières* 113: 1-278.

- PERKOVSKY E. E., RASNITSYN A. P., VLASKIN A. P. & TARASCHUK M. V. 2007 — A Comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. *African Invertebrates* 48: 229-245.
- PHILPOTT A. 1923 — A study of the venation of the New Zealand species of Micropterygidae. *Transactions and Proceedings of the New Zealand Institute* 54: 155-161.
- PRATT R. C., MORGAN-RICHARDS M. & TREWICK S. A. 2008 — Diversification of New Zealand weta (Orthoptera: Ensifera; Anostostomatidae) and their relationships in Australasia. *Philosophical Transactions of the Royal Society B* 363:3427-3437.
- RATNASINGHAM S. & HEBERT P. D. N. 2007 — BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>). *Molecular Ecology Notes* 7: 355-364.
- RONQUIST F. & HUELSENBECK J. P. 2003 — MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572-1574.
- ROTA J. & WAGNER D. L. 2006 — Predator mimicry: metalmark moths mimic their jumping spider predators. *PLoS ONE* 1: e45.
- SÉRET B. 2007 — Les poisons d'eau douce de Nouvelle-Calédonie: implications biogéographiques de récentes découvertes. In: Najt, J. & Matile, L. (eds), *Zoologia Neocaledonica*, 4. *Mémoires du Muséum national d'Histoire naturelle* 171: 369-378.
- SHARMA P. & GIRIBET G. 2010 — The curious relationships of New Caledonia and tropical Gondwana: insights from opiliofauna (Arachnida: Opiliones). Abstract only: VI Southern Connection Congress, Bariloche.
- SCHELLART W. P., KENNETT B. L. N., SPACKMAN W. & AMARU M. 2009 — Plate reconstructions and tomography reveal a fossil lower mantle slab below the Tasman Sea. *Earth and Planetary Science Letters* 278: 143-151.
- SOLTIS D. E. & SOLTIS P. S. 2004 — *Amborella* not a "basal angiosperm"? Not so fast! *American Journal of Botany* 91: 997-1001.
- STRANDBERG J. & JOHANSON K. A. 2010 — The historical biogeography of *Apsilochorema* (Trichoptera, Hydrobiosidae) revised, following molecular studies. *Journal of Zoological Systematics and Evolutionary Research* 49: 110-118.
- TENNYSON A. J. D., WORTHY T. H., JONES C. M., SCOFIELD R. P. & HAND S. J. 2010 — Moa's Ark: Miocene fossils reveal the great antiquity of moa (Aves: Dinornithiformes) in Zealandia. *Records of the Australian Museum* 62: 105-114.
- THIEN L. B., BERNHARDT P., GIBBS G. W., PELLMYR O., BERGSTRÖM I. G., GROTH I. & MCPHERSON G. 1985 — The pollination of *Zygogynum* (Winteraceae) by a moth, *Sabatinca* (Micropterigidae): an ancient association? *Science* 227: 540-543.
- TILLYARD R. J. 1923 — On the larva and pupa of the genus *Sabatinca*. *Transactions of the Entomological Society of London* 70: 437-453.
- TREWICK S., BRESCIA F. & JORDAN C. 2009 — Diversity and phylogeny of New Caledonian *Placostylus* land snails; evidence from mitochondrial DNA, in GRANDCOLAS P. (ed.), *Zoologia Neocaledonica* 7. Biodiversity studies in New Caledonia. *Mémoires du Muséum national d'Histoire naturelle* 198: 421-436.
- TUSKES P. M. & SMITH N. J. 1984 — The life history and behaviour of *Epimartyria pardella* (Micropterigidae). *Journal of the Lepidopterist's Society* 38: 40-46.
- VIETTE P. 1978 — Contribution à l'étude des Micropterigidae (7^e note). Un nouveau *Sabatinca* de Nouvelle-Calédonie. *Bulletin mensuel de la Société Linnéenne de Lyon* 47: 174-175.
- WAGSTAFF S. J. & DAWSON M. I. 2000 — Classification, Origin, and patterns of diversification of *Corynocarpus* (Corynocarpaceae) inferred from DNA sequences. *Systematic Botany* 25: 134-149.
- WALKER F. 1863 — List of the specimens of lepidopterous insects in the collection of the British Museum. Part XXVIII. Tortricites & Tineites. British Museum (Natural History), London: 287-561.
- WANG M., ZHAO Y. & REN D. 2009 — New fossil caddisfly from Middle Jurassic of Daohugou, Inner Mongolia, China (Trichoptera: Philopotamidae). *Progress in Natural Science* 19: 1427-1431.
- WALLIS G. P. & TREWICK S. A. 2009 — New Zealand phylogeography: evolution on a small continent. *Molecular Ecology* 18: 3548-3580.
- WHALLEY P. E. S. 1978 — New taxa of fossil and recent Micropterigidae with a discussion of their evolution and a comment on the evolution of Lepidoptera (Insecta). *Annals of the Transvaal Museum* 31: 71-86.
- WRIGHT S. D., YONG C. G., DAWSON J. W., WHITTAKER D. J., GARDNER R. C. 2000 — Riding the ice age El Nino? *Pacific biogeography and evolution of Metrosideros subg. Metrosideros* (Myrtaceae) inferred from nuclear ribosomal DNA. *Proceedings of the National Academy of Sciences of the United States of America* 97: 4118-4123.
- ZELLER-LUKASHORT H. C., KURZ M. E., LEES D. C. & KURZ M. A. 2007 — A review of *Micropterix*, Hubner 1825 from northern and central Europe (Micropterigidae). *Nota lepidopterologica* 30: 235-298.

APPENDIX 1

Taxon sampling. Geographic details and accession numbers, and BOLD index numbers (cluster reference numbers) for the samples analysed. N/A: short sequences do not qualify for barcodes but the sequences are accessible in the public project MICSA of BOLD (<http://www.boldsystems.org/index.php>).

Taxon	Country	Locality data	Latitude	Longitude	BOLD Sample ID	BOLD Process ID	Genbank Accession No	BOLD Index No
<i>Hypomartyria micropteroides</i>	Chile	Aguas Calientes, Parque Nacional Puyehue	-40,733	-72,301	CCDB-02227-A07	MICOW103-09	N/A	N/A
<i>Austromartyria porphyrodes</i>	Qld, Australia	The Crater NP	-17,433	149,483	CCDB-02228-H05	MICOW282-10	HM379296	BOLD:AAJ7589
<i>Zealandopterix zonodoxa</i>	New Zealand	Puketi Forest	-35,214	173,793	CCDB-02223-C08	MICOW032-09	GU662992	BOLD:AAE3184
<i>Aureopterix micans</i>	New Caledonia	Mts Koghis Niooli	-22,177	166,509	CCDB-08380-B03	MICOW398-10	HQ575019	BOLD:AAA6109
<i>Aureopterix sterops</i>	Qld, Australia	Mandena Meteorological Station, Kuranda	-16,818	145,663	CCDB-02223-G01	MICOW073-09	HM431791	BOLD:AAJ7598
<i>Tasmantrix fragilis</i>	NSW, Australia	Barrengarry Mountain	-34,681	150,507	CCDB-02223-F02	MICOW062-09	GU662975	BOLD:AAF8642
<i>Tasmantrix thula</i>	Qld, Australia	Henrietta Ck, Palmerston Hwy	-17,600	145,750	CCDB-02227-B01	MICOW109-09	HM424669	BOLD:AAG6620
<i>Sabatinca vietiei</i>	New Caledonia	Mts Koghis	-21,177	166,508	CCDB-08380-A01	MICOW384-10	HQ575008	BOLD:AAD5916
<i>Sabatinca vietiei</i>	New Caledonia	Riv Bleue, Pont Germain	-22,102	166,658	CCDB-08380-E02	MICOW433-10	HQ575049	BOLD:AAD5916
<i>Sabatinca vietiei</i>	New Caledonia	Mt. Panié	-20,6	164,8	Y1_micro_Sabatinca_01	MLPJ049-11	AB608899	BOLD:AAD5916
<i>Sabatinca vietiei</i>	New Caledonia	Pocqueraux	-21,733	165,898	CCDB-02227-B12	MICOW120-09	HM424674	BOLD:AAD5916
<i>Sabatinca</i> n. sp. 45	New Caledonia	Mt Rembai upper roadway	-21,584	165,843	CCDB-08380-C12	MICOW419-10	HQ575038	BOLD:AAD5915
<i>Sabatinca</i> n. sp. 45	New Caledonia	Mt Do summit road	-21,760	166,000	CCDB-08380-G02	MICOW457-10	HQ575064	BOLD:AAD5915
<i>Sabatinca</i> n. sp. 45	New Caledonia	Table Unio	-21,564	165,769	CCDB-08380-G03	MICOW458-10	HQ575065	BOLD:AAD5915
<i>Sabatinca</i> n. sp. 44	New Caledonia	Mt Do	-21,761	166,000	CCDB-02227-C01	MICOW121-09	GU663019	BOLD:AAD5917
<i>Sabatinca</i> n. sp. 44	New Caledonia	Mt Do	-21,758	166,000	CCDB-02227-D09	MICOW141-09	GU663023	BOLD:AAD5917
<i>Sabatinca</i> n. sp. 44	New Caledonia	Mts Koghis	-21,177	166,508	CCDB-08380-E04	MICOW435-10	HQ575051	BOLD:AAD5917
<i>Sabatinca</i> n. sp. 32	New Caledonia	Aoupinie	-21,153	165,320	CCDB-02227-D01	MICOW133-09	HM424681	BOLD:AAG6633
<i>Sabatinca</i> n. sp. 32	New Caledonia	Aoupinie roadway	-21,160	165,318	CCDB-08380-C05	MICOW412-10	HQ575032	BOLD:AAG6633
<i>Sabatinca</i> n. sp. 39	New Caledonia	Plateau de Dogny	-21,621	165,885	CCDB-02223-D08	MICOW044-09	GU662985	BOLD:AAD5913
<i>Sabatinca</i> n. sp. 7	New Caledonia	Aoupinie roadway	-21,160	165,318	CCDB-08380-C09	MICOW416-10	HQ575035	BOLD:AAF8640
<i>Sabatinca</i> n. sp. 7	New Caledonia	Aoupinie summit roadway	-21,183	165,300	CCDB-02227-E03	MICOW147-09	GU663024	BOLD:AAF8640
<i>Sabatinca</i> n. sp. 7	New Caledonia	Plateau de Dogny summit stream	-21,620	165,875	CCDB-08380-A10	MICOW393-10	HQ575015	BOLD:AAF8640
<i>Sabatinca</i> n. sp. 5	New Caledonia	Haute Pourina	-22,057	166,625	CCDB-02227-B05	MICOW113-09	HM424671	BOLD:AAG6622
<i>Sabatinca</i> n. sp. 58	New Caledonia	Mandjelia summit roadway	-20,396	164,532	CCDB-08380-D12	MICOW431-10	HQ575047	BOLD:AAM1540
<i>Sabatinca</i> n. sp. 21	New Caledonia	Plateau de Dogny	-21,620	165,875	CCDB-02227-C09	MICOW129-09	HM424679	BOLD:AAG6630
<i>Sabatinca</i> n. sp. 22	New Caledonia	Mt Do	-21,758	166,000	CCDB-02227-C10	MICOW130-09	GU663020	BOLD:AAG6631
<i>Sabatinca</i> n. sp. 22	New Caledonia	Dzumac road junction	-22,033	166,467	CCDB-02227-C11	MICOW131-09	GU663021	BOLD:AAG6631
<i>Sabatinca</i> n. sp. 37	New Caledonia	Riv Bleue, Pont Germain	-22,105	166,657	CCDB-02227-D04	MICOW136-09	GU663022	BOLD:AAF8637
<i>Sabatinca</i> n. sp. 37	New Caledonia	Dzumac	-22,033	166,475	CCDB-02223-D12	MICOW048-09	GU662984	BOLD:AAF8637
<i>Sabatinca</i> n. sp. 15	New Caledonia	Plateau de Dogny	-21,620	165,875	CCDB-02227-C02	MICOW122-09	HM424675	BOLD:AAG6627
<i>Sabatinca</i> n. sp. 10	New Caledonia	Pic d'Amoa	-20,956	165,291	CCDB-02227-B08	MICOW116-09	HM424673	BOLD:AAG6624
<i>Sabatinca</i> n. sp. 10	New Caledonia	Plateau de Dogny track	-21,624	165,868	CCDB-08380-C01	MICOW408-10	HQ575029	BOLD:AAM1537
<i>Sabatinca</i> n. sp. 12	New Caledonia	Mt Rembai gully	-21,581	165,837	CCDB-08380-E01	MICOW432-10	HQ575048	BOLD:AAM1541

<i>Sabatinca</i> n. sp. 12	New Caledonia	R Bleue Pont Germain	-22,105	166,657	CCDB-02227-B11	MICOW119-09	N/A	N/A
<i>Sabatinca</i> n. sp. 18	New Caledonia	Dzumac road below saddle	-22,088	166,447	CCDB-02227-C06	MICOW126-09	HM424678	BOLD:AAG6629
<i>Sabatinca</i> n. sp. 11	New Caledonia	Mt Do	-21,761	166,000	CCDB-02227-B09	MICOW117-09	GU663018	BOLD:AAG6625
<i>Sabatinca</i> n. sp. 11	New Caledonia	Dzumac road junction	-22,033	166,467	CCDB-02227-B10	MICOW118-09	GU663034	BOLD:AAG6626
<i>Sabatinca</i> n. sp. 11	New Caledonia	Les Bois du Sud, Gahnia inflorescence	-22,173	166,764	CCDB-08380-B02	MICOW397-10	HQ575018	BOLD:AAG6626
<i>Sabatinca</i> n. sp. 46	New Caledonia	Monts des Koghis	-22,183	166,502	CCDB-02223-H10	MICOW094-09	N/A	N/A
<i>Sabatinca</i> n. sp. 46	New Caledonia	Monts des Koghis	-22,183	166,502	CCDB-02223-H11	MICOW095-09	N/A	N/A
<i>Sabatinca</i> n. sp. 46	New Caledonia	Monts des Koghis	-22,183	166,502	CCDB-02223-E01	MICOW049-09	HM431787	BOLD:AAF8638
<i>Sabatinca</i> n. sp. 29	New Caledonia	Mts Koghis	-22,178	166,507	CCDB-02227-C12	MICOW132-09	HM424680	BOLD:AAG6621
<i>Sabatinca</i> n. sp. 29	New Caledonia	Mt Do summit road	-21,760	166,000	CCDB-08380-A09	MICOW392-10	HQ964333	BOLD:AAG6621
<i>Sabatinca</i> n. sp. 47	New Caledonia	Dzumac road junction	-22,033	166,467	CCDB-02227-D06	MICOW138-09	HM424683	BOLD:AAG6635
<i>Sabatinca</i> n. sp. 20	New Caledonia	Mts Koghis	-21,177	166,508	CCDB-08380-B05	MICOW400-10	HQ575021	BOLD:AAM1534
<i>Sabatinca</i> n. sp. 43	New Caledonia	Plateau de Dogny	-21,620	165,875	CCDB-02227-D07	MICOW139-09	N/A	BOLD:AAG6636
<i>Sabatinca</i> n. sp. 43	New Caledonia	Aoupinie	-21,183	165,300	CCDB-02227-E06	MICOW150-09	GU663025	BOLD:AAG6636
<i>Sabatinca</i> n. sp. 48	New Caledonia	Mt Rembai gully	-21,581	165,837	CCDB-08380-C11	MICOW418-10	HQ575037	BOLD:AAM1539
<i>Sabatinca</i> n. sp. 48	New Caledonia	Plateau de Dogny	-21,620	165,875	CCDB-02227-D12	MICOW144-09	N/A	N/A
<i>Sabatinca</i> n. sp. 48	New Caledonia	Mt Rembai	-21,579	165,840	CCDB-08380-B09	MICOW404-10	HQ575025	BOLD:AAM1536
<i>Sabatinca delobeli</i>	New Caledonia	Mt Mou, Sanatorium	-22,075	166,332	CCDB-02223-D06	MICOW042-09	HM431783	BOLD:AAJ7712
<i>Sabatinca</i> n. sp. 28	New Caledonia	Col d' Amieu	-21,591	165,802	CCDB-08380-B06	MICOW401-10	HQ575022	BOLD:AAM1535
<i>Sabatinca</i> n. sp. 6	New Caledonia	Table Unio	-21,564	165,769	CCDB-02227-B06	MICOW114-09	HM424672	BOLD:AAG6623
<i>Sabatinca</i> n. sp. 6	New Caledonia	Mt Rembai	-21,579	165,840	CCDB-08380-B07	MICOW402-10	HQ575023	BOLD:AAG6623
<i>Sabatinca</i> n. sp. 17	New Caledonia	Mt Rembai gully	-21,581	165,837	CCDB-08380-C10	MICOW417-10	HQ575036	BOLD:AAG6628
<i>Sabatinca</i> n. sp. 17	New Caledonia	Table Unio	-21,564	165,769	CCDB-02227-C05	MICOW125-09	HM424677	BOLD:AAG6628
<i>Sabatinca kristenseni</i>	New Caledonia	Les Bois du Sud, Gahnia inflorescence	-22,173	166,764	CCDB-08380-E05	MICOW436-10	HQ575052	BOLD:AAN0338
<i>Sabatinca</i> n. sp. 36	New Caledonia	Riv Bleue, Pont Germain	-22,105	166,657	CCDB-02227-D03	MICOW135-09	N/A	N/A
<i>Sabatinca</i> n. sp. 31	New Caledonia	Plateau de Dogny	-21,621	165,885	CCDB-02223-D07	MICOW043-09	HM431784	BOLD:AAF8635
<i>Sabatinca</i> n. sp. 50	New Caledonia	Dzumac road junction	-22,033	166,467	CCDB-02227-E02	MICOW146-09	N/A	N/A
<i>Sabatinca</i> n. sp. 49	New Caledonia	Mt Humboldt source	-21,883	166,417	CCDB-02227-E01	MICOW145-09	HM424684	BOLD:AAG6637
<i>Sabatinca</i> n. sp. 4	New Caledonia	Mt Rembai lower stream	-21,579	165,840	CCDB-08380-B08	MICOW403-10	HQ575024	BOLD:AAA6113
<i>Sabatinca</i> n. sp. 4	New Caledonia	Plateau de Dogny track waterfall	-21,624	165,868	CCDB-08380-B12	MICOW407-10	HQ575028	BOLD:AAA6113
<i>Sabatinca</i> n. sp. 4	New Caledonia	Plateau de Dogny track waterfall	-21,624	165,868	CCDB-08380-B11	MICOW406-10	HQ575027	BOLD:AAA6113
<i>Sabatinca</i> n. sp. 33	New Caledonia	Plateau de Dogny	-21,620	165,875	CCDB-02227-D02	MICOW134-09	HM424682	BOLD:AAG6634
<i>Sabatinca demissa</i>	New Zealand	Pureora Forest	-38,551	175,702	CCDB-02223-D01	MICOW037-09	HM431779	BOLD:AAJ7709
<i>Sabatinca incongruella</i>	New Zealand	Cherry Bay, Qn Charlotte Sound	-41,171	174,184	CCDB-02223-C12	MICOW036-09	HM431778	BOLD:AAJ7601
<i>Sabatinca chrysargyra</i>	New Zealand	Jackson/Arawhata confluence	-44,052	168,719	CCDB-02223-A08	MICOW008-09	GU663002	BOLD:AAE7760
<i>Sabatinca chrysargyra</i>	New Zealand	L Matheson	-43,444	169,968	CCDB-02223-A09	MICOW009-09	GU663003	BOLD:AAE7760
<i>Sabatinca chrysargyra</i>	New Zealand	Lake Harris track	-44,717	168,1847	CCDB-08380-D10	MICOW429-10	HQ575045	BOLD:AAE7760
<i>Sabatinca aemula</i>	New Zealand	Fergusson's Bush	-42,924	170,759	CCDB-02223-A01	MICOW001-09	GU663009	BOLD:AAE7760
<i>Sabatinca aemula</i>	New Zealand	Mt Hercules	-43,177	170,456	CCDB-02223-A04	MICOW004-09	GU663007	BOLD:AAE7760
<i>Sabatinca aemula</i>	New Zealand	Flora Saddle, Mt Arthur	-41,193	172,732	CCDB-02223-A02	MICOW002-09	GU663005	BOLD:AAE7760
<i>Sabatinca aenea</i>	New Zealand	Puhipuhi Val	-42,239	173,753	CCDB-02223-B06	MICOW018-09	HM431776	BOLD:AAJ7728

<i>Sabatinca ianthina</i>	New Zealand	Fergusson's Bush	-42,924	170,759	CCDB-02223-B02	MICOW014-09	N/A	N/A
<i>Sabatinca ianthina</i>	New Zealand	Flora Saddle, Mt Arthur	-41,193	172,732	CCDB-02223-B03	MICOW015-09	HQ964331	BOLD:AAI0993
<i>Sabatinca ianthina</i>	New Zealand	track above Kapuni Lodge	-39,331	174,092	CCDB-02223-B01	MICOW013-09	HM431775	BOLD:AAI0992
<i>Sabatinca aurella</i>	New Zealand	Bullock Ck	-42,094	171,391	CCDB-02223-A11	MICOW011-09	GU662999	BOLD:AAD9806
<i>Sabatinca aurella</i>	New Zealand	Whakanui track	-41,290	174,989	CCDB-02223-A10	MICOW010-09	GU663004	BOLD:AAD9806
<i>Sabatinca doroxena</i>	New Zealand	Otaki Forks	-40,870	175,234	CCDB-02223-B04	MICOW016-09	GU663000	BOLD:AAG6373
<i>Sabatinca doroxena</i>	New Zealand	Gollans Valley	-41,318	174,908	CCDB-02223-B05	MICOW017-09	GU662996	BOLD:AAG6373
<i>Sabatinca chalcophanes</i>	New Zealand	Te Ponanga Saddle	-39,010	175,740	CCDB-02223-B09	MICOW021-09	GU662993	BOLD:AAF1818
<i>Sabatinca chalcophanes</i>	New Zealand	Fox Glacier	-43,492	170,041	CCDB-02223-B11	MICOW023-09	GU662995	BOLD:AAF1818
<i>Sabatinca chalcophanes</i>	New Zealand	5-mile track	-41,341	174,971	CCDB-02223-B10	MICOW022-09	GU662994	BOLD:AAF1818
<i>Sabatinca caustica</i>	New Zealand	Bald Hill	-46,187	167,825	CCDB-02223-B07	MICOW019-09	GU662997	BOLD:AAJ7699
<i>Sabatinca caustica</i>	New Zealand	Catlins R. Val	-46,429	169,452	CCDB-02223-C06	MICOW030-09	N/A	N/A
<i>Sabatinca caustica</i>	New Zealand	Ulva Island	-46,930	168,122	CCDB-02223-B08	MICOW020-09	GU662998	BOLD:AAJ7699
<i>Sabatinca quadrijuga</i>	New Zealand	Mt Cargill, Dunedin	-45,813	170,554	CCDB-02223-C02	MICOW026-09	HM431777	BOLD:AAJ7594
<i>Sabatinca calliarcha</i>	New Zealand	Lake Matheson	-43,444	169,968	CCDB-02223-D04	MICOW040-09	HM431781	BOLD:AAJ7704
<i>Sabatinca calliarcha</i>	New Zealand	Kohaihai track	-41,105	172,104	CCDB-02223-D03	MICOW039-09	N/A	N/A
<i>Sabatinca lucilia</i>	New Zealand	Waitakere Range	-36,935	174,520	CCDB-02223-D02	MICOW038-09	HM431780	BOLD:AAJ7607
<i>Sabatinca heighwayi</i> (larva)	New Zealand	Harwoods Hole, Canaan	-40,944	172,882	CCDB-02227-A05	MICOW101-09	HM424668	BOLD:AAJ7605
<i>Sabatinca heighwayi</i>	New Zealand	Harwoods Hole, Takaka Hill	-40,950	172,870	CCDB-08380-G05	MICOW460-10	HQ575067	BOLD:AAJ7605
<i>Micropterix wockei</i>	Greece	Nafpaktos	38,475	21,889	CCDB-02227-H03	MICOW183-09	HM424688	BOLD:AAK6451
<i>Micropterix aureatella</i>	Sweden	Omskoldsviks commun, Skuleskogen, Langra, Brook ravine in mixed forest	63,089	18,498	CCDB-02223-E06	MICOW054-09	GU662983	BOLD:AAE7973
<i>Micropterix aureoviridella</i>	Austria	Kufstein	47,582	12,183	CCDB-02227-F11	MICOW167-09	HM424686	BOLD:AAK6447
<i>Micropterix calthella</i>	England	Morden Meadows	51,192	0,173	CCDB-02227-H01	MICOW181-09	GU663032	BOLD:AAE0036
<i>Micropterix tunbergella</i>	Switzerland	La Neuveville, La Baume	47,067	7,081	CCDB-02227-G01	MICOW169-09	GU663030	BOLD:AAD7678
<i>Palaeomicroides</i> sp.	Taiwan	Pilu (Bilyu) Sacred Tree, Taroko National Park	24,106	121,235	CCDB-02227-C04	MICOW124-09	HM424676	BOLD:AAI2600
<i>Palaeomicroides</i> sp.	Taiwan	Fu-Shan Research Station	24,759	121,552	CCDB-02223-F06	MICOW066-09	GU662972	BOLD:AAI5093
<i>Issikiomartyria</i> sp.	Japan	Shirabiso-touge, Nagano			YI_micro_Issikisp_01	MLPJ001-11	AB608851	BOLD:AAP1376
<i>Issikiomartyria plicata</i>	Japan	Irisawai, Nagano			YI_micro_Issiki_07	MLPJ009-11	AB608859	BOLD:AAW9196
<i>Kurokoptyx dolicherata</i>	Japan	Morimachi, Shizuoka			YI_micro_kuroko_01	MLPJ011-11	AB608861	BOLD:AAP1045
<i>Kurokoptyx</i> cf. <i>dolicherata</i>	Japan	Ishikiri, Shizuoka			YI_micro_kuroko_04	MLPJ014-11	AB608864	BOLD:AAP1045
<i>Neomicroptyx bifurca</i>	Japan	Mt. Hoyoshidake, Kagoshima			YI_micro_Neo_01	MLPJ020-11	AB608870	N/A
<i>Neomicroptyx matsumurana</i>	Japan	Zakogawa, Nagano			YI_micro_Neo_12	MLPJ031-11	AB608878	BOLD:AAP1040
<i>Paramartyria semifasciella</i>	Japan	Tamakiguchi, Wakayama			YI_micro_parama_03	MLPJ046-11	AB608896	BOLD:AAP1316
<i>Paramartyria immaculatella</i>	Japan	Mt. Kiyosumi, Chiba			YI_micro_parama_01	MLPJ044-11	AB608894	BOLD:AAJ2500
<i>Epimartyria pardella</i>	United States	Prairie La	40,775	-124,000	CCDB-02223-F04	MICOW064-09	GU662976	BOLD:AAF1263
<i>Epimartyria auricrinella</i>	Canada	Ch. Saint Lois, 3 km from Saint-Lois de Chamez, Gatineau Park	45,392	-76,095	CCDB-02227-F05	MICOW161-09	GU663027	BOLD:AAD9116
<i>Epimartyria auricrinella</i>	Canada	Lac Brule	46,0881	-74,2788	jflandry0725	MEC725-04	GU095821	BOLD:AAD9116
<i>Rhyacophila manistee</i>	USA	Nebo Rt. 622, Virginia	36,565	-81,264	EPA0522	MDA521-08	JN200746	BOLD:AAB2361
<i>Rhyacophila invaria</i>	USA	Gulch Stream, Virginia	38,579	-77,097	EPA0349	MDA349-08	JN200741	BOLD:AAE3600
<i>Rhyacophila angelita</i>	Canada	23 km E Churchill, Ramsay Creek	58,731	-93,78	06Probe1037	DSTRI047-06	GU114273	BOLD:AAA6495

<i>Rhyacophila glaberrima</i>	USA	West Riverside, Virginia	38,58	-77,096	EPA0103	MDA103-08	JN200740	BOLD:AAB2280
<i>Apsilochorema hwangi</i>	China				AY490798	GBMH0795-06	AY490798	BOLD:AAJ8757
<i>Psilochorema leptoharpax</i>	New Caledonia		39,2	176,62	AO1	GBMH4479-08	AM902790	BOLD:AAD8819
<i>Alloeocentrella</i> sp	New Caledonia				EF395048	GBMH2601-07	EF395048	BOLD:AAW1889
<i>Helicophya neocaledonia</i>	New Caledonia				EF395032	GBMH2617-07	EF395032	BOLD:AAE6977
<i>Wormaldia moesta</i>	USA	Fishing Creek, Maryland	39,526	-77,389	EPA0560	MDA559-08	JN200799	BOLD:AAB7150
<i>Chimarra marginata</i>	No data				FM998346	GBMH7657-10	FM998346	BOLD:AAM2015
<i>Hydrobiosella uncinata</i>	New Caledonia				BX2		FN179047	
<i>Stenopsyche marmorata</i>	Japan	Sakawa River, Kanagawa Prefecture				GBMH5556-09	AB308379	BOLD:AAD5174

Owlfies of New Caledonia, *Suhpalacsa caledon* McLachlan, 1871 (Neuroptera: Ascalaphidae)

Roland Dobosz ⁽¹⁾ & Ábrahám Levente ⁽²⁾

⁽¹⁾ Upper Silesian Museum, Natural History Department, Sobieskiego 2, PL 41-902 Bytom, Poland
dobosz@muzeum.bytom.pl

⁽²⁾ Rippl-Rónai Museum, Natural History Department, H-7400 Kaposvár, P.O. Box 70, Hungary
labraham@smmi.hu

ABSTRACT

Suhpalacsa caledon McLachlan, 1871 is an endemic species found only in New Caledonia. In this paper the authors made a richly illustrated morphological description of both sexes and its unknown larva. Habitat and mapping of distribution of the species are also given. The distribution of the genus is restricted to Australia and Melanesian archipelagoes.

RÉSUMÉ

Planipennes de Nouvelle-Calédonie *Suhpalacsa caledon* McLachlan, 1871 (Névroptères : Ascalaphidae).

Suhpalacsa caledon McLachlan, 1871 est une espèce endémique trouvée seulement en Nouvelle-Calédonie. Dans cet article, les auteurs font une description morphologique richement illustrée de l'espèce, de ses deux sexes et de sa larve inconnue. Ils indiquent aussi l'habitat et la cartographie de la répartition des espèces. La distribution du genre est limitée à l'Australie et aux archipels mélanésien.

INTRODUCTION

New Caledonia (Kanaky) is located in the region of Melanesia in the southwest Pacific approximately 1.200 km east of Australia and 1.500 km northwest of New Zealand, made up of a main island (Grande Terre), the Loyalty Islands, and several smaller islands, their territories about 19.000 km².

The Grande Terre is by far the largest, elongated northwest-southeast, 350 km long island. A mountain range runs the length of the island, the highest peaks over 1.500 meters.

The climate of the islands is subtropical, rainfall about 1.500 mm yearly. The western side of the Grande Terre lies in the rain shadow of the central mountains. Temperature ranges from 17-27°C. There are two main seasons: a dry season, and a warm and wet season.

New Caledonia is considered one of the world's most important and critically endangered hotspots as is an ancient fragment of the Gondwana super-continent. It separated from Australia at the end of the Cretaceous and from New Zealand in the mid-Miocene. This has led to a long period of evolution in near complete isolation. Although, New Caledonia's fauna and flora includes a few species that reached its shores from Australia and other islands, however, the isolation of New Caledonia was not absolute. Some species migration both into, and out of, the island was facilitated by the rise and fall of sea levels due to ice ages, which in turn caused islands and land bridges to form between New Caledonia and its neighbors, the Solomon Islands, Vanuatu and Australia. Thus, new species had the opportunity to reach New Caledonia, while species of Gondwanan origin penetrate further eastward into the Pacific Island region (Boyer & Giribet 2007).

In New Caledonia only one ascalaphid species was found, described as *Suhpalacsa caledon* McLachlan, 1871 based on a female specimens. Later, only female specimens were recorded and characterized again in the neuropterological literature (Weele 1909). The genus *Suhpalacsa* was considered to be rich in species from Africa, SE Asia and Australia (Weele 1909, New 2003). However, *Suhpalacsa* species were found only in Australia, African and SE Asian species are belonging to different genera (Ábrahám 2008).

The main aim of this investigation on the only known endemic ascalaphid species from New Caledonia is to describe the male, which are different from the female because of sexual dimorphism, and larva as well as to clear the faunal connections in the future.

MATERIAL AND METHODS

This study is based on 24 specimens deposited in the following entomological collections:

BPBM Bernice P. Bishop Museum, Honolulu, Hawaii, USA.

SCM Rippl-Rónai Museum, Kaposvár, Hungary.

USMB Upper Silesian Museum, Bytom, Poland.

Data from the original locality labels are cited *in extenso* for series of specimens. Additional data and attachments are given in square parentheses.

SYSTEMATIC PART

Family ASCALAPHIDAE Lefèbvre, 1842

Genus **SUHPALACSA** Lefèbvre, 1842

Type species. *S. flavipes* (Leach, 1814)

INCLUDED SPECIES — From Australia and New Caledonia, 21 *Suhpalacsa* species were described. After a generic revision (New 1984), 15 valid *Suhpalacsa* species remained; the other 6 species were replaced into genera *Megacmonotus* New, 1984, *Pilacmonotus* New, 1984 and *Suphalomit*. From New Caledonia only one endemic species, *Suhpalacsa caledon* McLachlan, 1871 is known (Weele 1909).

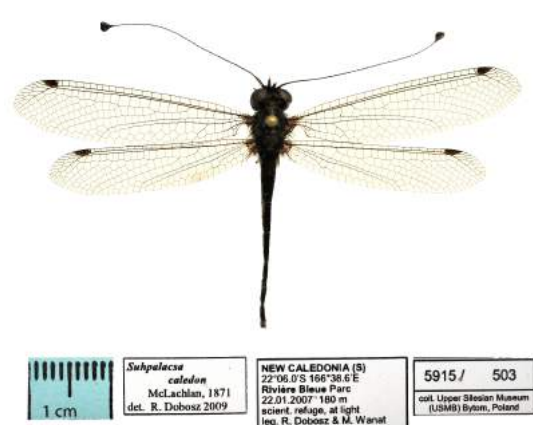
DIFFERENTIAL DIAGNOSIS — The genus *Suhpalacsa* is characterised by narrow, elongate wings, parallel costal and inner margins and straight or slightly curved anal forewing area (New 1984).

***Suhpalacsa caledon* McLachlan, 1871**

Suhpalacsa caledon McLachlan, 1871: 258.

MATERIAL EXAMINED — [BPBM]: 1 ♀ New Caledonia [S]: Forêt de Thi [22°11'03"S 166°31'59"E], 100-300 m, 24-25.III.1961, J. Sedlacek; [BPBM]: 1 ♂ New Caledonia [S]: Mt. Koghi [22°10'36"S 166°30'30"E], 500 m, I.1963, N.L.H. Krauss; [BPBM]: 1 ♀ New Caledonia [S]: Col de Mouriance [Mouirange] [22°12'48"S 166°39'57"E], 2.II.1963, N.L.H. Krauss; [USMB]: 1 ♂ 1 ♀ New Caledonia [S]: Rivière Bleue Parc [22°05'S 166°38'E], 22-25.01.2004 150-300 m, leg. Dariusz Skibiński; [USMB]: 1 ♀ New Caledonia (S), 22°05'S 166°38'E Haute Rivière Bleue: Track to La Tranchée, 180-330 m, 23.01.2004, leg. M. Wanat; [USMB]: 1 ♀ New Caledonia (N) 21°09'S 165°19'E Aoupinié 420-530 m road to sawmill 7.02.2004 leg. M. Wanat; [USMB]: 1 ♂ New Caledonia (S), 22°06.0'S 166°38.6'E Rivière Bleue Parc, 3-5.01.2006, 180 m, scient.[ifc] refuge, leg. Ernest Minnema; [USMB]: 2 ♀ New Caledonia (N), 20°32.0'S 164°20.0'E, Koum, 20.01.2007, at light, leg. Alain Renevier; [USMB]: 1 ♂ New Caledonia (S) 20°06.0'S 166°38.6'E Rivière Bleue Parc 180 m, scient.[ifc] refuge at light, 22.01.2007 leg. R. Dobosz, M. Wanat; [USMB]: 5 ♂ 1 ♀ New Caledonia (S) 20°05'S 166°38'E Rivière Bleue Parc 190-330 m, track to La Tranchée 22.01.2007 leg. R. Dobosz; [SCM]: 1 ♀ New Caledonia (S) 20°05'S 166°38'E Rivière Bleue Parc 190-330 m, track to La Tranchée 22.01.2007 leg. R. Dobosz; [SCM]: 1 ♂ 1 ♀ New Caledonia (S) 20°05'S 166°38'E Rivière Bleue Parc 190-330m, track to La Tranchée 22.01.2007 leg. R. Dobosz; [USMB]: 3 ♂ 1 ♀ New Caledonia (S) 20°05'S 166°38'E Rivière Bleue Parc 190-330 m, track to La Tranchée 23.01.2007 leg. R. Dobosz.

LARVAL MATERIAL EXAMINED — [USMB]: 2nd instar: New Caledonia (S), Mt. Koghi 22°10.7'S 166°30.4'E, rainforest sitting, 16.12.2006, leg. R. Dobosz; [USMB] 1st instar: New Caledonia (S), Pic du Pin forêt, 280 m, 22°14.9'S 166°49.7'E, 25.12.2006. sifting leg. M. Wanat & R. Dobosz; [USMB] 2nd instar New Caledonia (S), Pic du Pin forêt, 280 m, 22°14.9'S 166°49.7'E, 25.12.2006. sifting leg. R. Dobosz & M. Wanat; [SCM]: 2nd instar New Caledonia (S), Pic du Pin forêt, 280 m, 22°14.9'S 166°49.7'E, 25.12.2006. sifting leg. R. Dobosz & M. Wanat.



FIGURES 1-2

Habitus of *Suhpalacsa caledon*. 1, male; 2, female.

MORPHOLOGICAL CHARACTERIZATION OF IMAGOS — Sexual dimorphism is present with respect to pubescence of the head, size of antenna, wings and abdomen, coloration of club and pattern of abdomen. Habitus of male and female (Figures 1, 2).

Head. Coloration of head same on both male and female. Vertex grey covered with long dense and shining black pubescence that sporadically mixed with white hairs, on female pubescence long dense and shining white that sporadically mixed with black hairs. Narrow shining black stripes on both sides of epicranial suture. Frons shining brown with indistinct pale yellowish pattern on ventral part. Hairs on frons of male moderately sparse black. Fronto-clypeal inflection with long dense tufts of black hairs. Frons of female with white hairs, its fronto-clypeal inflection also with long dense tufts of white hairs centrally and a few black ones laterally. Gena shining black next to frons and clypeus yellow next to eye and mandible. Ventral part of gena with short sparse and white hairs on both male and female. Clypeus and labrum yellow. Clypeo-genal inflection with short sparse white hairs. Ventral margin of labrum with short, sparse, shining and ochraceous hairs curved to mouthparts. Mandible yellow with black apex. Maxillae and labial palpi yellow. Palpar segments with sparse white hairs. Apical 2 palpar joints with sporadic stiff and black setae. Occiput black, hairless. Postorbital sclerite black next to vertex, yellow beside occiput, hairless. Eye large, divided by suture-like inflection transversally. Dorsal part of eye larger than ventral part. Antenna 22-23 mm on males, 20-21 mm on females, about 2/3x shorter than distance between base of forewing and pterostigma. Scape and pedicel black with long dense and blackish pubescence. Long dense tufts of black hairs between scapes. Black to brown flagellar segments equal, bare. Distal part of flagellar segments broadened out at joins. Club of male yellow ventrally and brown dorsally, club of female yellow on both sides only last segments brownish annulated. Club subglobular-shaped with flattened apex and with short, black smoothing verticals. Bristle of club black.

Thorax. Pronotum, mesonotum and metanotum of male shining brown to yellowish with short sparse brown hairs, of female shining brown to grey with short sparse and white hairs. Lateral projection of pronotum with long and brown hairs. Sides greyish to white with long soft dense and white hairs. Pleura of male with long soft and brown hairs on both pterothorax, of female with long soft and white hairs on meso- and metascutum.

Legs. Long and robust. Coloration and pubescence of coxa and trochanter similar to sides. Femur yellowish to brown with long and white hairs and some distal black bristles. Tibia brown, somewhat shorter than femur with short stiff shining and black bristles. Tarsi black with stiff shining and black bristles. Tarsal segments 1-4 equal; segment 5 somewhat shorter than segments 1-4 combined. Tibial spurs and claws black. Tibial spurs on fore leg as long as tarsal segments 1-2 together, on middle leg 1.5 segments, on hind leg basitarsus combined.

Wings. Forewing: 28-30 mm long and 6.5-7 mm wide of male; 30-32 mm long and 7-7.5 mm wide of female. Hindwing: 24-25 mm long and 5 mm wide of male; 26-27 mm long and 6.5 mm wide of female. Apex with rounded apices, anal area of forewing obtusely angled and along hind margin of anal area slightly concave. Membrane transparent. Pterostigma as short as wide on forewing, brownish with 4 brown cross veins and longer than wide on hindwing. C yellow, Sc blackish basally, yellow distally. Other longitudinal veins black except yellow anal veins basally, cross veins also black. C with short dense smoothing and black setae. Setae on other veins sparse and black. Apical area beyond vein Sc+R with three rows of cells. In front of origin of Rs 5-6 radial cross-veins in forewing and 2-3 in hindwing.

Coloration of hindwing similar to forewing. Hind pterostigma with 5 cross-veins. On male ambient vein with long, soft and brown hairs, on female with long soft and white hairs.

Abdomen. 28-29 mm long of male, length of female abdomen 17-18 mm. Tergites of male unicolor reddish-brown, sternites with white meal-like powder. Tergite 1 divided dorsally, brown with long soft and shining brown hairs. Tergite 2 as long as wide with long, brown hairs. Other tergites 2x longer than wide with sparse hairs and short setae.

Tergal segments of female greyish with distinct velvety black pattern. Two triangle-shaped and V-shaped pattern on third tergite in dorsal view (Figure 3). Hairs on tergite 1 long soft dense and greyish, on tergite 2 long soft and white. Sternal segments greyish. Hairs on sternite 1 with long and white, on sternite 2 short and white, other sternites short shining and black.



FIGURE 3

Pattern on the third tergite of female abdomen
(Photo: Ernest Minnema).

Male genitalia (Figures 4, 5). In lateral view tergite 9 triangular-shaped, brown centrally yellowish marginally covered with sparse short black setae marginally. Ectoprocts oval, with moderately long stiff and black setae. In ventral view sternite 9 rhomboid-shaped with small tongue-shaped projections covered with sparse white hairs and with some long and black ones laterally. Gonarcus arch-like, fused with parameres. Caudal margins of parameres verrucosed. Pelta small. Pulvini bag-like with moderately long gonosetae.

Female genitalia (Figure 6). Tergite 9 sub-rhomboid, greyish to yellow in lateral view. Setae sparse, short and black. Ectoprocts with pair of convex black plates with moderately dense black setae. Hairs on caudal margin dense shining and yellowish. Distivalvae yellow with stiff and black hairs. Ventrovalvae thumb-like in ventral view, grey with long stiff and black hairs.

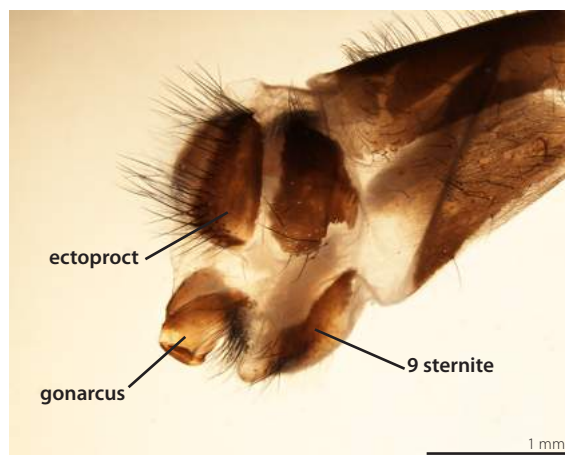


FIGURE 4

Male genitalia *Suhpalacsa caledon* in lateral view.

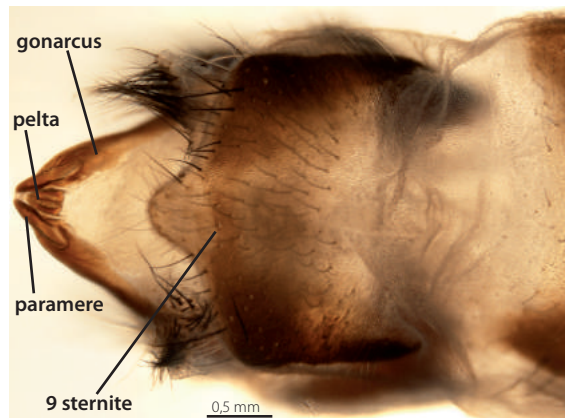


FIGURE 5

Male genitalia *Suhpalacsa caledon* in ventral view.

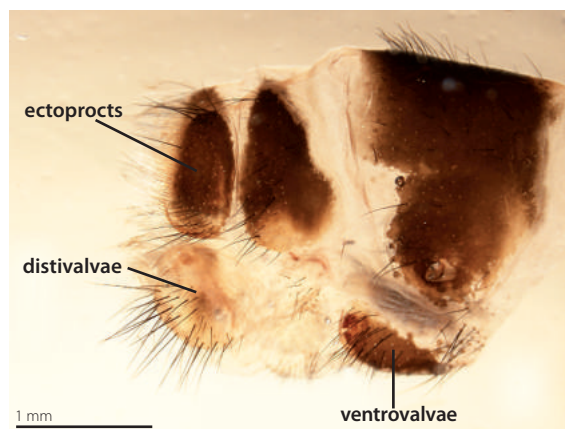


FIGURE 6

Female genitalia of *Suhpalacsa caledon* in lateral view.

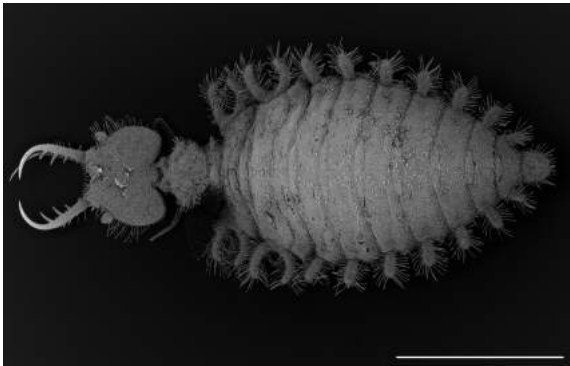


FIGURE 8
Habitus of the *Suhpalacsa caledon* larva (SEM) (scale bar: 5 mm).

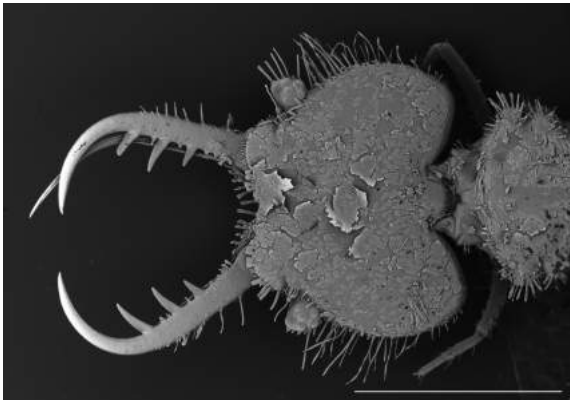


FIGURE 9
Head and prothorax in dorsal view (scale bar: 2 mm).

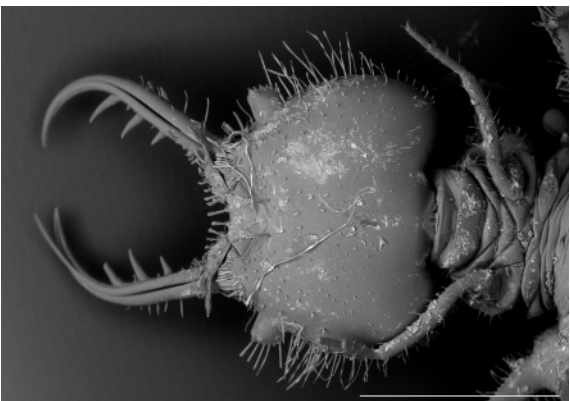


FIGURE 10
The same in ventral view (scale bar: 2 mm).

TABLE 1
Measurement of the characteristic part of the larva in mm.

LARVAE	LENGTH OF MANDIBULA	LENGTH OF HEAD	WIDTH OF HEAD
1st instar	1.15	1.35	1.65
2nd instar	2.0	2.2	2.8

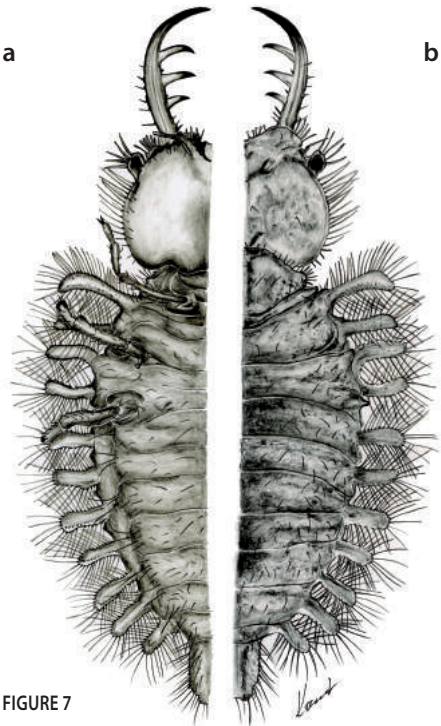


FIGURE 7
Habitus of the *Suhpalacsa caledon* larva: a, ventral view; b, dorsal view (drawing).

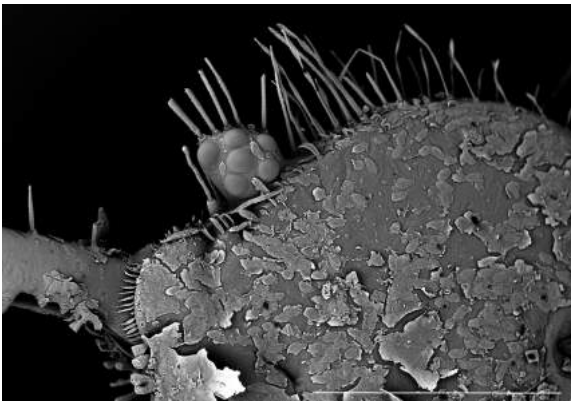


FIGURE 11
Part of head: eye, antenna and base of mandible in dorsal view (scale bar: 1 mm).



FIGURE 12
The same in ventral view (scale bar: 1 mm).



FIGURE 15
Fore leg of the larva (scale bar: 5 mm).

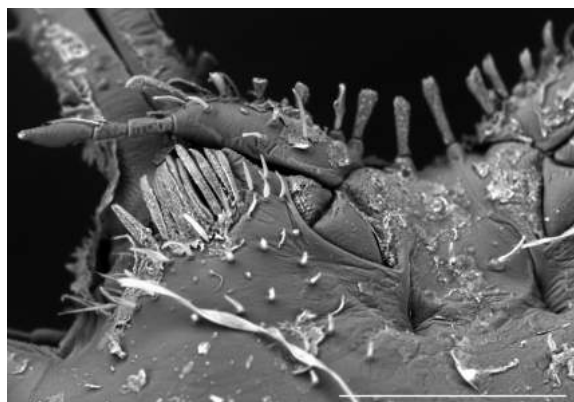


FIGURE 13
Prelabial lobe and labial palpi in ventral view (scale bar: 5 mm).

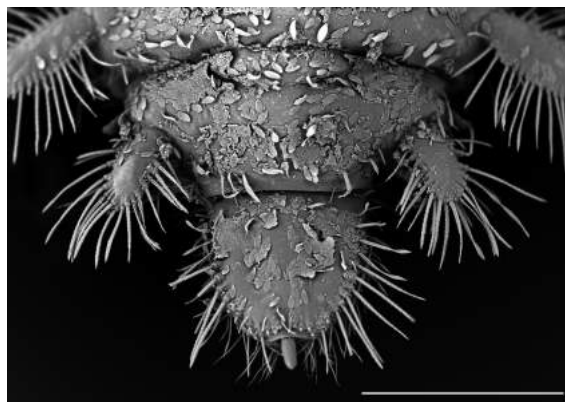


FIGURE 16
Tergite 9 in dorsal view (scale bar: 5 mm).

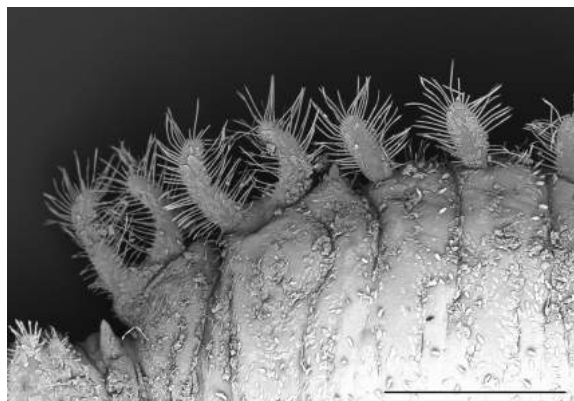


FIGURE 14
Scoli on meso, metathorax and 1-2 tergal segments in dorsal view (scale bar: 2 mm).



FIGURE 17
Sternite 9 in ventral view (scale bar: 5 mm).



FIGURE 18
Typical habitat of
Suhpalacsa caledon at
River Bleue Reserve
(Photo: Dariusz
Skibiński).



FIGURE 19
Male *Suhpalacsa*
caledon in resting
position (Photo:
Roland Dobosz).



FIGURE 20
Female
Suhpalacsa
caledon in
resting position
(Photo: Ernest
Minnema).

DESCRIPTION OF LARVAE — Habitus of the 2nd instar larvae (Figures 7, 8) and measurements (Table 1).

Head. in dorsal view slightly longer than wide (Figure 9), in ventral view as in Figure 10. Jaws a bit shorter than the length of head. V-shaped brown pattern right above on dorso-posterior emargination and white long hairs on its lateral margin. Antenna short, scape and pedicel cylindrical, flagellum filiform, 6 dorsal brown stemmata of eyes (Figure 11). Mandible robust, curved with 3 prominent teeth. First tooth the longest one, third tooth the shortest one, only half length of the first one. Ends of teeth and the apex of mandible brown. Only a few tooth-like dolichaster on mesal margin of mandible. In ventral view brownish indistinct pattern on both sides of central inflection. Posterior inflection shallow with central protrusion. One ventral brown stemmata of eyes (Figure 12). Prelabial lobe longer than 3-segmented labial palpi (Figure 13)

Thorax. yellow with indistinct brown pattern centrally. Meso- and metathorax shorter centrally than laterally with strong cylindrical scoli covered with long white bristles (Figure 14). Anterior scoli with flattened apical part and larger than posterior one. Obtuse projection on latero-posterior margin of mesothorax. Scoli on metathorax equally. Metathorax with lateral peaked projections. Legs yellow with brown claws (Figure 15).

Abdomen. yellow with brown indistinct pattern centrally on tergites. Tergite 9 shield-shaped, 1.5x longer than wide with lateral white bristles (Figure 16). Sternite segments also yellow without pattern. Sternite 9 elongate nearly parallel-sided with white hairs (Figure 17).

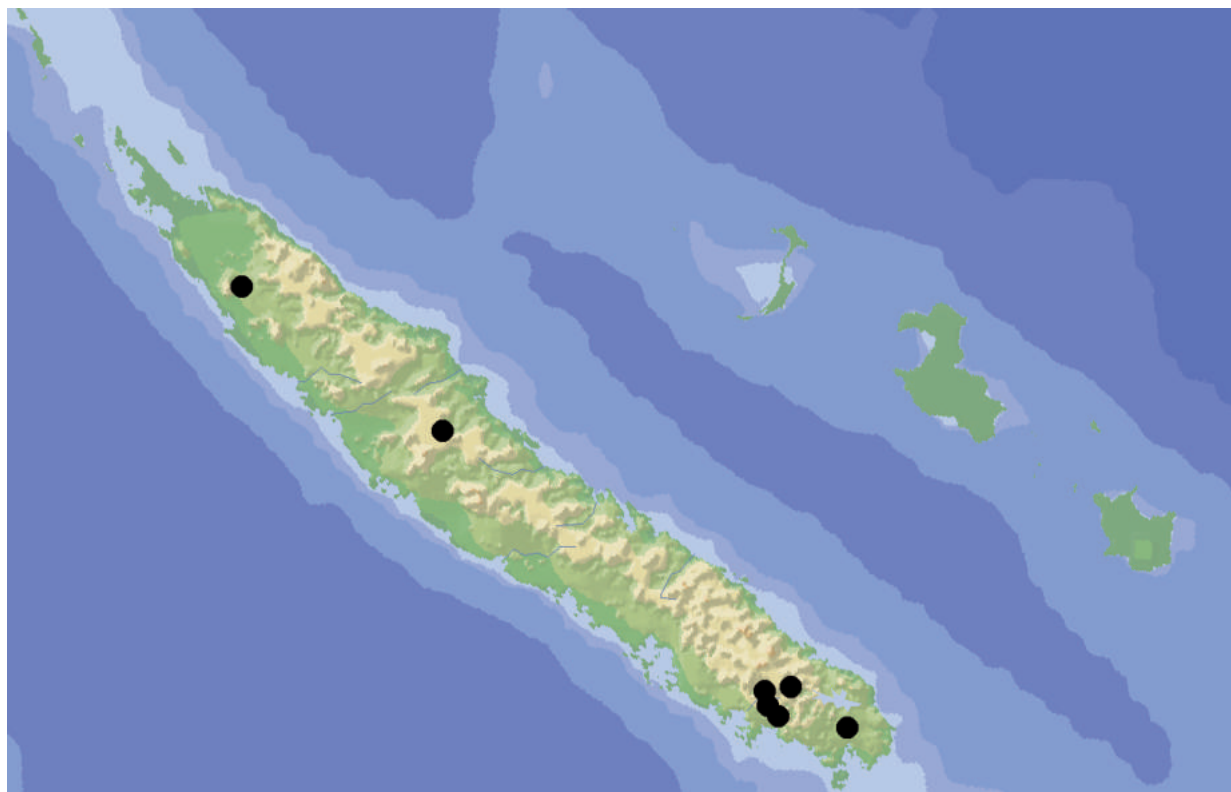


FIGURE 21

Distribution map of *Suhpalacsa caledon* in New Caledonia.

HABITAT AND DISTRIBUTION — All larvae were collected in a rain forest by sifting litter at root of death and living trees from leaves spreading. The imagoes fly in the sunny places (gaps, clear cutting) in rain forests (Figure 18), in paths across rain forests and on the border of rain forests with the scrubs or maquis. Most males and females were collected at flying or sitting on the branch of scrub in the sunny places (Figures 19, 20). The imagoes are active in sunshine. Only three specimens came to the light in Koum and in Rivière Bleue Parc. The light trap in Rivière Bleue Parc was placed in maquis near the scientific refuge.

It seems to be an endemic species for New Caledonia (Figure 21).

ACKNOWLEDGMENTS

The authors express their grateful thanks to Dr. Marek Wanat for helping in recording, Mrs. Malwina Roszkowska for taking SEM photos, Mr. Ernst Minnema and Mr. Dariusz Skibiński for the photos in the field and Dr. Jarosław Kania for excellent drawing of the larva. The authors would also thanks Dr. Shepherd Myers from the Bishop Museum for a loan scientific material.

The first author especially thank late Henri Blaffart (petite croix pour les morts) (Association Dayu Biik), Christian Mille and Sylvie Cazerès (IAC, Pocquereux), Hervé Jourdan (IRD), and Martin Brinkert (Forestry, Pondimié) for their help and advice during my field work in New Caledonia. I wish to express my sincere thanks to Anne-Claire Goarant and David Paulaud (Direction de l'Environnement, Province Sud) and Jean-Jérôme Cassan (Direction du Développement Économique et de l'Environnement, Province nord) for the permits to collect neuropteran material in New Caledonia. Jörn Theuerkauf, Paweł Krzyżyński, Marek Wanat, Tomasz Blaik are thanked for their great logistic help, advice, and nice company during field expeditions.

REFERENCES

- ÁBRAHÁM L. 2008 — Ascalaphid Studies VI. New genus and species from Asia with comments on genus *Suhalacsa* (Neuroptera: Ascalaphidae). *Somogyi Múzeumok Közleményei* 18: 69-76.
- BOYER S. L. & GIRIBET G. 2007 — A new model Gondwanan taxon: systematics and biogeography of the Gondwanan harvestman family Pettalidae (Arachnida, Opiliones, Cyphophthalmi), with a taxonomic revision of genera from Australia and New Zealand. *Cladistics* 23: 337-361.
- MCLACHLAN R. 1871 — An attempt towards a systematic classification of the family Ascalaphidae. *Journal of the Linnean Society of London, Zoology* 11: 219-276.
- NEW T. R. 1984 — Revision of the Australian Ascalaphidae. *Australian Journal of Zoology*, Supplementary Series 100: 1-86.
- NEW T. R. 2003 — The Neuroptera of Malesia. *Fauna Malesiana*, vol. 4. Brill, Leiden. VIII + 204 p.
- VAN DER WEELE H. W. 1909 — Ascalaphiden monographisch bearbeitet. *Collection Zoologique Selys Longchamps* 8: 1-326.

Redefinition of the cricket genus *Protathra* Desutter-Grandcolas, 1997 (Orthoptera, Grylloidea, Phalangopsidae), with description of the calling song of *Protathra centralis* Desutter-Grandcolas, n. sp.

Laure Desutter-Grandcolas ⁽¹⁾, Tony Robillard ⁽¹⁾ & Jérémy Anso ^(1,2)

⁽¹⁾ Muséum national d'Histoire naturelle, Institut de Systématique, Évolution, Biodiversité, ISYEB - UMR 7205 CNRS, UPMC, EPHE, CP 50, 45, rue Buffon, 75005 Paris, France
desutter@mnhn.fr

⁽²⁾ IMBE, Aix-Marseille Université, UMR CNRS IRD Avignon Université, UMR 237 IRD, Centre IRD Nouméa - BP A5, 98848 Nouméa Cedex, Nouvelle-Calédonie

ABSTRACT

The cricket genus *Protathra* Desutter-Grandcolas, 1997a is redefined, adding male characters (stridulatory apparatus, genitalia) to the original diagnosis. The study of newly collected specimens allows precisifying the definition of the type species *Protathra gigantea* Desutter-Grandcolas, 1997a, and to describe an additional, new species for the genus, *Protathra centralis* Desutter-Grandcolas, n. sp. from Aoupinié and Amoa mountains. A key to identify Phalangopsidae crickets from New Caledonia is given. The calling song of *Protathra gigantea* is described, documenting the acoustic behavior of New Caledonian Phalangopsidae for the first time.

RÉSUMÉ

Redéfinition du genre de grillons *Protathra* Desutter-Grandcolas, 1997 (Orthoptera, Grylloidea, Phalangopsidae), avec la description du chant d'appel de *Protathra centralis* Desutter-Grandcolas, n. sp.

Le genre de grillons *Protathra* Desutter-Grandcolas, 1997a est redéfini, avec l'ajout des caractères des mâles (appareil stridulatoire, genitalia) à la diagnose originale. L'étude de spécimens nouvellement collectés permet de préciser la définition de l'espèce type *Protathra gigantea* Desutter-Grandcolas, 1997a, et de décrire une espèce nouvelle supplémentaire pour le genre, *Protathra centralis* Desutter-Grandcolas, n. sp. originaire du massif de l'Aoupinié et du Pic Amoa. Une clé d'identification des Phalangopsidae de Nouvelle-Calédonie est proposée. Le chant d'appel de *Protathra gigantea* est décrit, ce qui constitue la première contribution sur le comportement acoustique des Phalangopsidae néocalédoniens.

INTRODUCTION

The Phalangopsidae crickets from New Caledonia include four genera, two probably endemic to the Grande Terre, *Caltathra* Otte, 1987 and *Protathra* Desutter-Grandcolas, 1997, and two largely distributed in Oceania, *Parendacustes* Chopard, 1924 (see Desutter-Grandcolas 2002) and *Pseudotrignidium* Chopard, 1915.

Protathra was originally described on females only (Desutter-Grandcolas 1997). Since then, additional material has been collected or found in Museum collections. These specimens proved to belong to the type species of the genus, *P. gigantea* Desutter-Grandcolas, 1997, but also to a species new to science, *P. centralis* Desutter-Grandcolas, n. sp., which is described here.

These new data allow to complete the diagnosis and description of *Protathra*, taking into account the characters of the males. Male genitalia clearly confirm that *Protathra* is close to *Caltathra*, as hypothesized earlier (Desutter-Grandcolas 2002). Both genera can however easily be separated by their morphology and male genitalia (see the key below).

Among New Caledonian phalangopsids, *Caltathra* is apterous and mute. *Parendacustes* has usually well-developed tegmina and stridulatory apparatus, and must be able to emit acoustic signals, but *P. lifouensis* Desutter-Grandcolas, 2002, which lives in cavities of calcareous shore (Desutter-Grandcolas 2002), is apterous. *Pseudotrignidium* forages on understorey plants, low trees and ferns and most species are able to call (Desutter-Grandcolas 1997b). Males *Protathra* are also able to call (Figure 3) and occupies the same habitat as *Caltathra* in new Caledonian rainforests (Desutter-Grandcolas 1997c, Fig. 4).

MATERIAL AND METHODS

MATERIAL

Extensive field work in New Caledonia for more than 30 years by MNHN field trips (Desutter-Grandcolas 1997a, b, c, 2002; Robillard *et al.* 2010) allowed a comprehensive cricket sampling in many localities of Grande Terre and the prospection of the Loyalty Islands (Lifou). Specimens were collected by sight only, by night and day, in order to observe their precise habitat and type of activity. Additional material from the Brisbane Museum, collected for biodiversity surveys of Southern New Caledonia, were also examined.

TAXONOMIC ANALYSIS

Male tegminal veins and cells were named according to homology statements proposed by Desutter-Grandcolas (2003). The apical field is very reduced in *Protathra*, and only C, D, E and perhaps F cell alignments (sensu Robillard & Desutter-Grandcolas 2004) can be identified (Figures 6, 13).

Male and female genitalia have been dissected in softened specimens by cutting the membranes between the paraprocts and the subgenital plate or between the ovipositor and the subgenital plate respectively; they have been observed after cleaning with cold KOH using a binocular Leica MZ12, at magnification up to 160, and then kept in glycerine in vials pinned under studied specimens. Male genitalia are named according to Desutter (1987), modified in Desutter-Grandcolas (2003).

ACOUSTIC RECORDING AND ANALYSIS

Males of *Protathra centralis* Desutter-Grandcolas, n. sp. have been recorded by T. Robillard (MNHN) with a Sony Handycam HDR-HC3 video recorder at dusk at Col d'Amieu. Calling songs were extracted from the video using the software Ulead Video Studio ver 11 and analyzed using the software Avisoft-SAS-Lab Pro version 4.40 (Specht 2008). Song description follows Ragge and Reynolds (1998).

ABBREVIATIONS

Morphology. FW, forewing; FI, II, III, fore, median, hindfemora; TI, II, III, fore, median, hindtibiae. Male genitalia: arc, ectophallic arc; ec. ap., ectophallic apodeme; ec. f., ectophallic fold; en. ap., endophallic apodeme; en. s., endophallic

sclerite; d.v., ectophallic dorsal valves; ps., pseudepiphallus; ps. m., median process of pseudepiphallus; ps. p., pseudepiphallic paramere; pr., paired processes of pseudepiphallus; r., rami. Male tegmina: 1A, first anal vein; CuA, anterior cubitus; di, diagonal vein (CuA1); MA, MP, anterior, posterior media veins; c1, c2, first, second cells of C alignment; mi, mirror (d1 cell); ch, chords; E, E cell alignment.

Institutions. MNHN, Muséum national d'Histoire naturelle, Paris; QMF, Queensland Museum, Brisbane, Australia.

Measurements (in mm, mean value in parentheses). LFIII, hindfemur length; LFW, forewing length; Lpron, pronotum length; LTIII, hindtibia length; Lovip, ovipositor length; wFW, forewing width at the level of mirror anterior angle; wpron, pronotum width (posterior margin).

SYSTEMATICS PART

KEY TO PHALANGOPSIDAE CRICKETS FROM NEW CALEDONIA

1. TIII with 3 inner and 4 outer subapical spurs 2
 – TIII with 2 inner and 3 outer subapical spurs *Parendacustes lifouensis* Desutter-Grandcolas, 2002
2. Species from small or medium size. Male and female apterous. Fastigium at the same level as the vertex. TI without a tympanum *Caltathra* Otte, 1987
 – Species of very large size. Female apterous. Male with short forewings covering less than half abdomen; stridulatory apparatus complete (harp and mirror crossed by several parallel veins; stridulatory file functional). Fastigium below the vertex, from which it is separated by a transverse furrow. TI with a small, outer tympanum *Protathra* Desutter-Grandcolas, 1997

Family PHALANGOPSIDAE Blanchard, 1845

Genus ***PROTATHRA*** Desutter-Grandcolas, 1997

Protathra Desutter-Grandcolas, 1997a: 150.

Type species. *Protathra gigantea* Desutter-Grandcolas, 1997a.

OTHER SPECIES INCLUDED — *Protathra centralis* Desutter-Grandcolas, n. sp. (Aoupinié).

DISTRIBUTION — *Protathra* is known from New Caledonia only, where it has been found in the Central mountains chain.

EMENDED DIAGNOSIS — Size very large; coloration variegated yellow and brown, legs annulated (Figure 1). Face yellow and brown; a wide longitudinal yellow band between median ocellus and clypeus distal margin (Figure 2). Eyes very protruding. Fastigium very narrow and separated from the vertex by a thin transverse furrow; median ocellus vertical, subapical on fastigium; lateral ocelli very close to each other, the distance between one lateral and the median ocelli much greater than the distance between the lateral ocelli. Scapes very large. Maxillary palpi moderately elongate; joint 3 smaller than joint 4; joint 5 the longest, truncate apically, regularly widened toward apex. Pronotum DD with a clear longitudinal median furrow; distal margin widely bordered with white setae (Figure 3); LL anterior angles raised dorsally, posterior angles truncate. TI with a small inner tympanum only; 2 apical spurs, the inner the longest. TII with 3 apical spurs, the ventral inner spur the longest, the dorsal outer spur missing. FIII with a thin apical part. TIII higher than wide; 3 inner and 4 outer subapical spurs; 3 inner and 3 outer apical spurs, the median spur the longest on both sides, median



FIGURES 1-5

Protathra gigantea Desutter-Grandcolas, 1997: **1**, male MNHN-EO-ENSIF3131, habitus; **2**, face coloration; **3**, right FW; **4**, supra anal plate; **5**, subgenital plate. Scale 1 mm for 1.

inner spur as long as one third to one half of basitarsomere III. TIII serrulated over their whole length with numerous, widely separate, very small spines. Basitarsomeres III very long; with two rows of few, small dorsal spines.

Male. Metanotum without setae and glandular pits. Tergites (Figure 1) and supra anal plate (Figure 4) without glandular areas. Forewings short, covering less than half of abdomen (Figure 1); dorsal and lateral fields separated by high MA; median area dorsal and flat, MP and CuA faint, CuP missing; lateral field narrow, narrowed in distal half, with faint and irregular veins, R close to MA and faint. Stridulatory apparatus complete and functional (Figures 6, 13): harp crossed by several oblique parallel veins; mirror crossed by several oblique or transverse veins. Male subgenital plate low, with a distinct bump at about mid length of lateral margin (Figures 7, 14); with a short distal, longitudinal, median furrow (Figure 5).

Male genitalia. Compact. Pseudepiphallic sclerite transverse (Figures 8, 15); median process broadly conical and completely sclerotized; on each side of the median process, a long and thin tube-shaped process with a bunch of long setae on its tip. Pseudepiphallic parameres large, thick and greatly sclerotized, bifid on distal margin (Figures 10, 16). Rami wide, separated from pseudepiphallic sclerite but almost in contact with it; with abruptly narrowed anterior part. Ectophallic dorsal valves short and sclerotized (Figure 9); ectophallic fold short, truncate apically; ectophallic apodemes wide and flat; ectophallic arc incomplete. No dorsal cavity. Endophallic sclerite U-shaped, with a faint median sclerotization (Figure 10).

Female. Apterous; ovipositor longer than FIII.

Female genitalia. Copulatory papilla triangular, heavily sclerotized (Figure 19).

CALLING SONG — According to observations of *P. gigantea*, the call of *Protathra* is a short echeme made of a few syllables emitted from dusk to night (Figure 11).

HABITAT — *Protathra* is a forest dwelling cricket, which forage on standing trees at night (Figure 12B); a small population of *P. gigantea* has been observed during the day hiding under a dead fallen tree (Figure 12A), males calling to attract nearby females (T. Robillard & F. Müller, pers. obs.).

RELATIONSHIPS — *Protathra* is most closely related to *Caltathra* Otte, 1987, as shown by the common features of their male genitalia (endophallic sclerite and apodeme, ectophallic valves) and morphology (TIII subapical and apical spurs). Both genera clearly constitute monophyletic entities, and their straightforward recognition using morphological characters justify their generic status (see below). Their sistership relation is supported by molecular data, as documented by a forth coming paper on cricket molecular phylogeny (Chintauan-Marquier, Legendre *et al.*, submit.).

Protathra gigantea Desutter-Grandcolas, 1997a

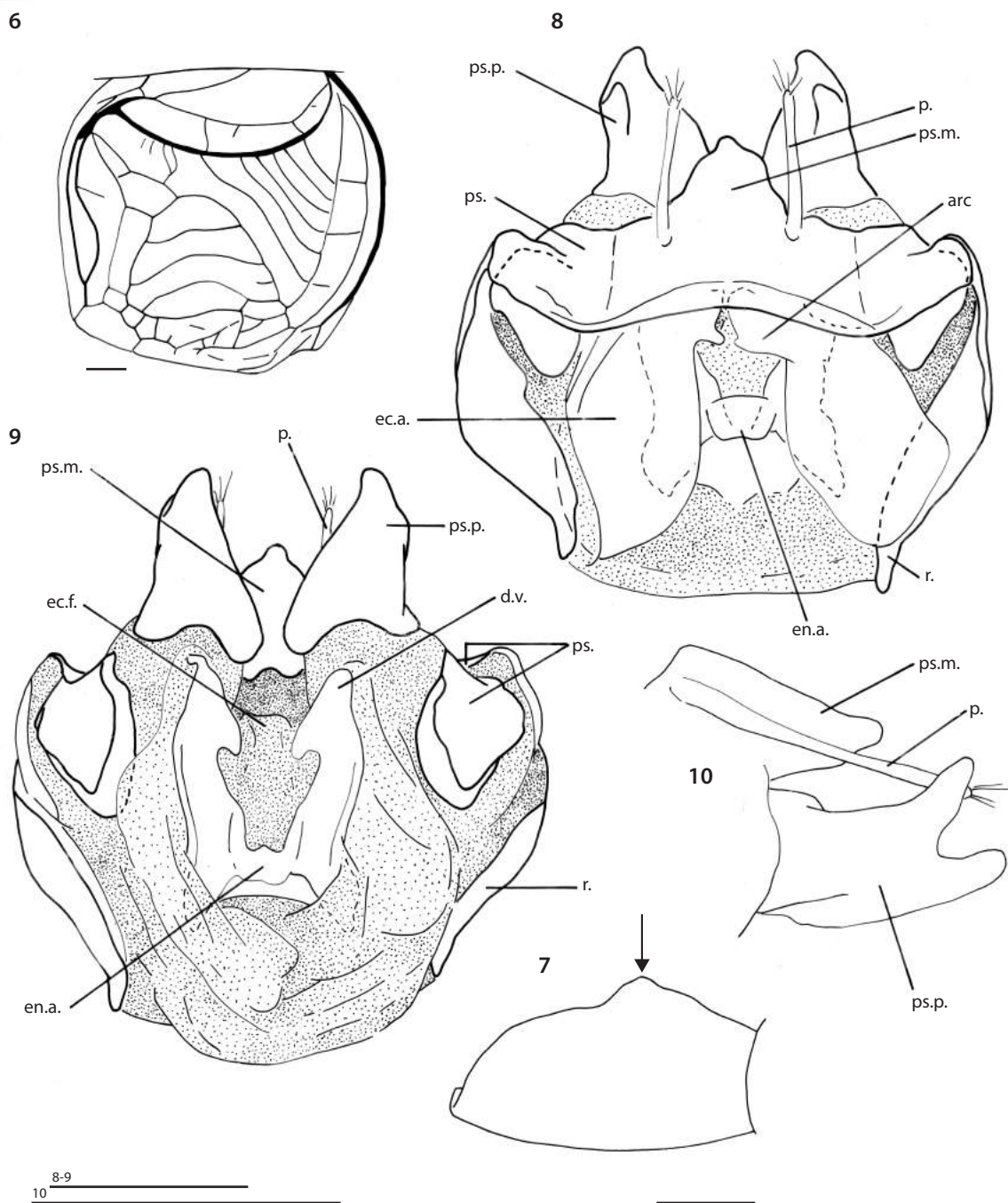
Figures 1-11, 12A

Desutter-Grandcolas, 1997a: 150.

TYPE MATERIAL — Holotype: New Caledonia, 3 km WNW Col d'Amieu, N. La Foa, 450-550 m, 1 female, forêt sempervirente, 18.ii.1994, nuit, sur tronc, L. Desutter-Grandcolas (MNHN-EO-ENSIF2846). Paratype, 1 female: Same locality and collector as the holotype, 1 female, 16.ii.1994, nuit, sur tronc (MNHN-EO-ENSIF2847).

ADDITIONAL MATERIAL EXAMINED — New Caledonia, 8 km NW Col d'Amieu, N. La Foa, Pied Table Unio (PK 8), 21°34'42"S 165°47'38"E, 450 m, 8.v.2008, 1 male, 3 females, fnFM29-32, jour, sous tronc mort, T. Robillard & F. Müller (MNHN-EO-ENSIF3127-3130). Same locality and collectors, 21°34'50"S 165°47'47"E, 450 m, 12.v.2008, 1 male, fnFM113 (MNHN-EO-ENSIF3131), 1 juvenile, fnTR220, nuit, sur tronc (MNHN).

TYPE LOCALITY — New Caledonia, 3 km WNW Col d'Amieu, N. La Foa, 450-550 m, rain forest.



FIGURES 6-10

Protathra gigantea Desutter-Grandcolas, 1997: **6**, male FW venation; **7**, male subgenital plate, lateral (right) (arrow, lateral bump); **8-10**, male genitalia, dorsal (**8**), ventral (**9**), lateral (left, **10**). Abbreviations: see material and methods. Scales 1mm.

EMENDED DIAGNOSIS — In addition to the characters indicated by Desutter-Grandcolas (1997):

Male. FWs short but with a complete stridulatory apparatus (Figures 1, 6): harp with 6 oblique parallel veins, mirror crossed by 2-3 transverse, parallel veins, file with 130-169 teeth. Lateral field with only one strong, longitudinal vein.

Male genitalia. Median and lateral processes of pseudepiphallus long, compared to those of *P. centralis* Desutter-Grandcolas, n. sp. (compare Figures 8, 10 and 15, 16); dorsal and ventral branches of paramere forceps equal in length (Figure 10).

EMENDED DESCRIPTION — In addition to the characters of the genus, and the specific characters given by Desutter-Grandcolas (1997a): TIII inner serrulation: no spine before subapical spur 1, and between subapical spurs 1 and 2, one to four spines in females (mean 2.5) and one to two spines in males (mean 1.3) between spurs 2 and 3, 23 to 29 spines in females (mean 25.8) and 22 to 24 in males (mean 23.3) above spur 3. TIII outer serrulation: no spine before spur 1, one to three spines in females (mean 1.2) and no spine in males between spurs 1 and 2, three to five spines in females (mean 3.7) and two to five spines in males (mean 3.5) between spurs 2 and 3, three to five spines in females (mean 4.3) and five to seven spines in males (mean 6) between spurs 3 and 4, 15 to 20 spines in females (mean 18.2) and 17 in males above spur 4. Basitarsomeres III with five to seven inner spines in females (mean 5.7) and three to six in males (mean 4.7), and 5 to 10 outer spines in females (mean 6.8) and 8 in males.

Male. FWs not covering half abdomen. Stridulatory apparatus (Figure 6): harp with 6 oblique, parallel veins; mirror triangular, anterior angle rounded, crossed by 2-3 veins; stridulatory file with 130-169 teeth (mean 149.5, n=2). Lateral field narrowed in distal half; only one, longitudinal, vein, parallel and close to MP; some very faint traces of additional, not parallel veins. Supra anal plate distal margin rounded, without elongate distal angles (Figure 4). Subgenital plate low and short, furrowed distally over 1/8 of its length (Figure 5); lateral bump as on Figure 7.

Male genitalia. Median process of pseudepiphallus reaching pseudepiphallic parameres mid length; lateral processes as long as three / fourth paramere length (Figures 8, 10). Branches of paramere forceps equal in length (Figure 10). See measurements table 1.

CALLING SONG — *Protathra gigantea* has a short calling song consisting of a short echeme (Figure 11A) comprising three to four syllables ($m=3.9\pm0.2$). Each echeme lasts for 129 ± 6 ms with a period of 1.34 ± 0.82 s. Syllables within echemes are of two types (Figure 11C): the first one is long (duration = 52 ± 8 ms, period = 74.4 ± 8.9 ms) and shows an indented amplitude profile, while the next syllables are shorter with a homogeneous amplitude profile (duration = 21.6 ± 5.6 ms, period = 35.9 ± 7.8 ms). The frequency spectrum shows a clear dominant peak at 3.23 ± 0.16 kHz, corresponding to the first harmonic (Figure 11B, D).

TABLE 1

Measurements (in mm) for *Protathra gigantea* Desutter-Grandcolas, 1997

	Lpron	wpron	LFW	wFW	LFIII	LTIII	File
Males	3.7-4.4	4.3-4.8	5.3-5.8	5.4-6.3	18.8-22.5	18.3-21.6	130-169
mean (n=2)	4.1	4.6	5.6	5.9	20.7	20	149.5

Protathra centralis Desutter-Grandcolas, n. sp.

Figures 12B, 13-21

TYPE MATERIAL — Holotype: New Caledonia, Massif de l'Aoupinié, avant barrière vers sommet, forêt sur pente, 21°10'52"S 165°18'06"E, 801m, 1 male, 17.v.2008, nuit, fn FM125, sur tronc, 1,5 m H, T. Robillard & F. Müller (MNHN-EO-ENSIF3126). Allotype: New Caledonia, Aoupinié, top camp, 21°11'S 165°19', 850m, 1 female, 2-3.xi.2001, G. Burwell &

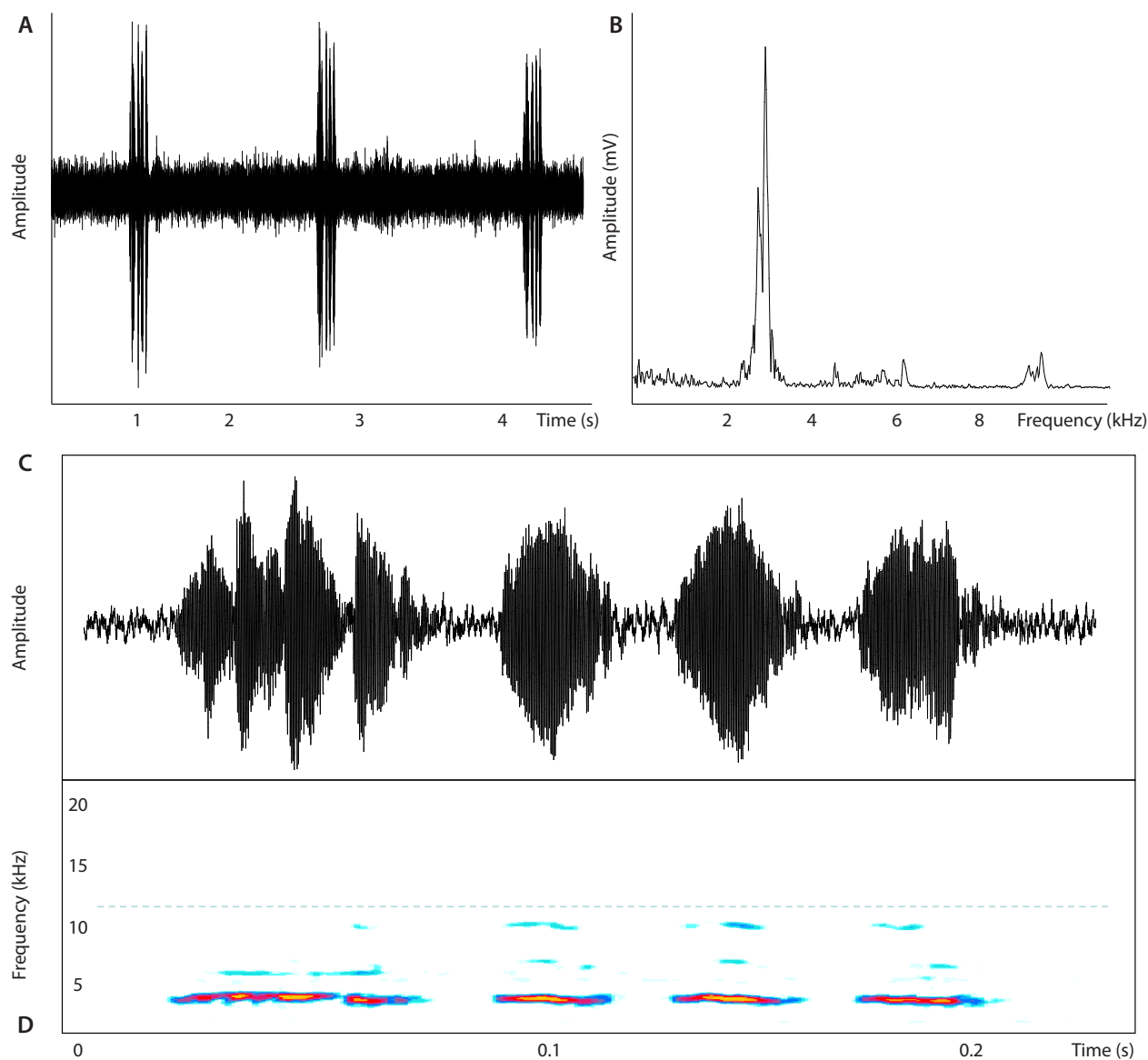


FIGURE 11

Protathra gigantea Desutter-Grandcolas, 1997, calling song: Oscillogram of three echemes (A); linear power spectrum of one syllable (B); oscillogram (C) and spectrogram (D) of one echeme.

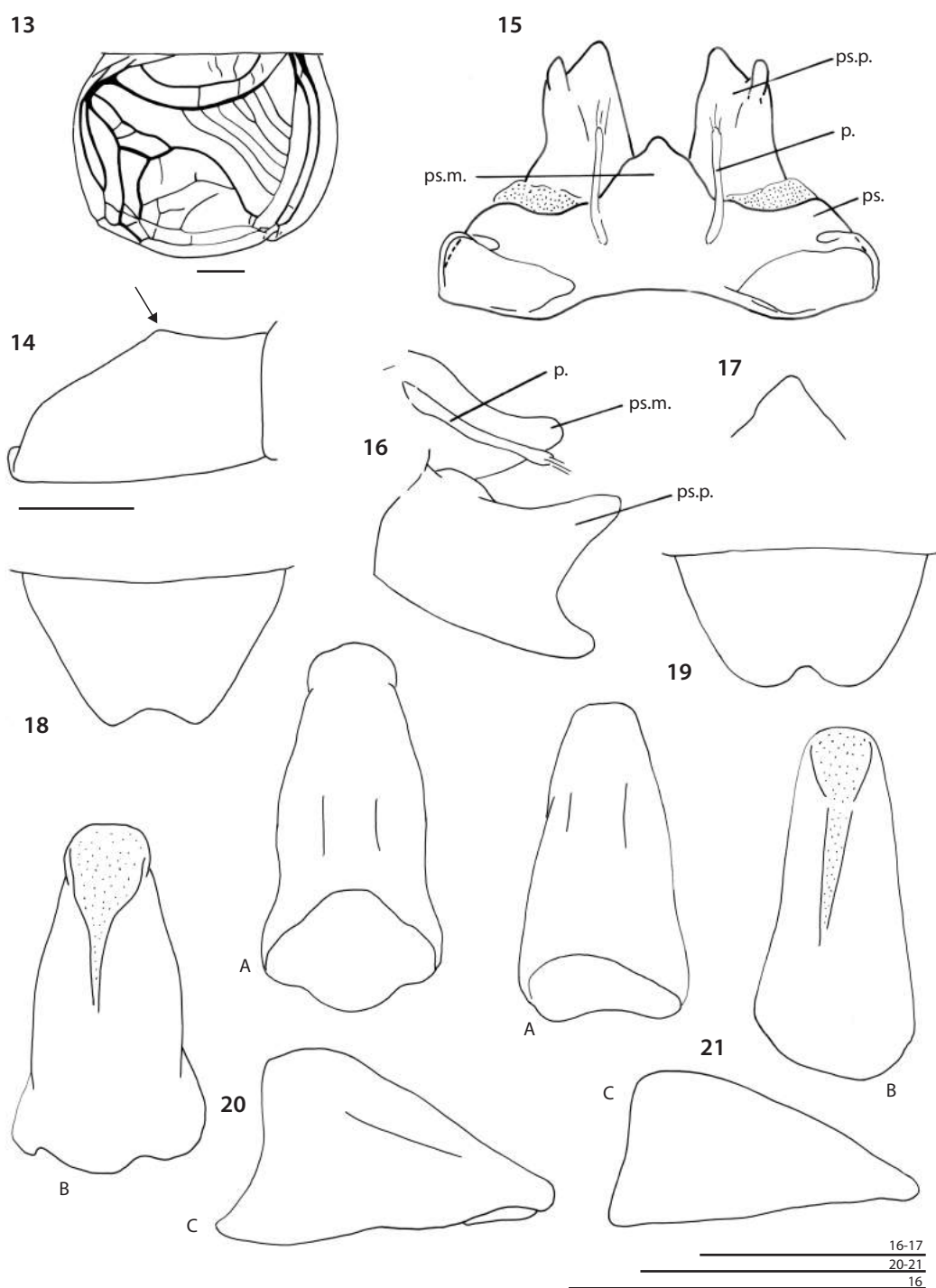
G. Monteith, hand collect (MNHN-EO-ENSIF3123). Paratypes, 2 males: Same data as the holotype, 1 male, fnTR267, tronc, 1,4m H, T. Robillard & F. Müller (MNHN-EO-ENSIF3125). Aoupinié top camp, 21°11'S 165°19'E, 850 m, 1 male, 2-3.xi.2001, C. Burwell & G. Monteith, molecular sampling LDG005 (MNHN-EO-ENSIF3124).

ADDITIONAL MATERIAL EXAMINED — New Caledonia, Pic d'Amoa, N slopes, 20°50'S 165°17'2, 500m, 1 male, 27.xi.2003-30.i.2004, G. Monteith, flight int. trap. New Caledonia, Aoupinié, top camp, 21°11'S 165°19', 850m, 1 female, 2-3.xi.2001, G. Burwell & G. Monteith, hand collect (QMF).



FIGURE 12

Protathra species in their natural environment: **A**, *P. gigantea* Desutter-Grandcolas, 1997, male calling in a fallen hollow tree; **B**, *Protathra centralis* Desutter-Grandcolas, n. sp. on tree trunk at night.



FIGURES 13-21

Protathra centralis Desutter-Grandcolas, n. sp.: **13**, male FW venation; **14**, male subgenital plate, lateral (right) (arrow, lateral bump); **15-17**, male genitalia, dorsal (**15**), lateral (left, **16**), male paratype, pseudepiphallic median process, dorsal (**17**); **18-19**, female subgenital plate, ventral, allotype (**18**), additional female (**19**); **20-21**, female copulatory papilla, dorsal (A), ventral (B), lateral (C), in female allotype (**20**) and additional female (**21**). Scales 1mm.

TYPE LOCALITY — New Caledonia, Aoupinié mountains.

ETYMOLOGY — Species named after the central location of Aoupinié mountains in New Caledonia.

DIAGNOSIS — Species very close to *P. gigantea*, from which it can be separated by its male genitalia (lateral processes of pseudepiphallus shorter, not reaching pseudepiphallic forceps, pseudepiphallic parameres wider, dorsal part of their forceps longer than ventral part).

DESCRIPTION — TIII inner serrulation: no spine before subapical spur 1; zero spine in females, zero to one spine in males (mean 0.2) between spurs 1 and 2; two to four spines in females (mean 2.5), two to six spines in males (mean 3.5) between spurs 2 and 3; 23–27 spines in females (mean 24.5), 22–27 spines in males (mean 23.8) above spur 3. TIII outer serrulation: no spine before spur 1; zero to three spines in males (mean 1.2) and females (mean 1.3) between spurs 1 and 2; two to four spines in females (mean 3), three to six spines in males (mean 4.2) between spurs 2 and 3; three to six spines in females (mean 4.5), four to six spines in males (mean 5) between spurs 3 and 4; 16 – 17 spines in females (mean 16.8), 17–22 spines in males (mean 18.7) above spur 4. Basitarsomeres III with five to six in females (mean 5.5), two to six in males (mean 5.3) inner spines, and five to eight in females (mean 6.8), seven to nine in males (mean 7.8) outer spines.

Coloration. Face light yellowish brown with a light yellow band between median ocellus and clypeus tip, bordered with black brown between the scapes; a wide brown band below each antennal pit, prolonged down to mandibula margin, connected or not to brown lateral margins of cheeks; head dorsum yellow between the eyes, with a thin transverse brown line posterior to fastigium and two irregular brown lines toward vertex; posterior margin of vertex brown; fastigium brown with a transverse V-shaped yellow line anterior to lateral ocelli. Pronotum black brown, with yellowish pyriform inscriptions, lighter margins, a pair of wide yellow spots close to anterior margin, a curved yellowish line lateral to inscriptions and a wide band of whitish setae along posterior margin; LL dark brown. Legs yellow and brown; FI with four dorsal flecks, ventral margin yellow, FII with three dorsal flecks, the basal one long, FIII with two apical rings, and three dorsal irregular flecks otherwise, Tibiae with four dark rings. Basitarsomeres I, II light brown, yellow at base; basitarsomeres III light brown. Abdomen yellow and brown, with transverse lines of black dots. Cerci light brown, inner side darker at base.

Male. FWs as on Figure 13; mirror crossed by 1–2 veins. Stridulatory file with 157–167 teeth ($n=2$, mean 162). FWs light brown, veins lighter; MA yellowish. Subgenital plate as on Figure 14.

Male genitalia. Median process of pseudepiphallus shorter than in *P. gigantea*, not reaching pseudepiphallic paramere mid length (Figure 16); paired processes shorter than in *P. gigantea*, going slightly beyond paramere mid length (Figure 15, 16); in lateral view, pseudepiphallic parameres wider and paramere forceps more asymmetrical, the dorsal branch longer than ventral one (Figure 16).

Female. Subgenital plate transverse, distal margin largely sinuate (Figure 18). Ovipositor longer than FIII.

Female genitalia. Copulatory papilla very similar to that of *P. gigantea* (Figure 20), with the same membranous part ventrally, and slight dorsal constriction; *P. centralis* papilla however somewhat shorter and wider than that of *P. gigantea* (see Desutter-Grandcolas 1997a, Figure 27). See measurements table 2.

REMARK — The male originating from Amoa is similar to males from Aoupinié, except for its much smaller size (compare measurements); as neither FW venation, nor male genitalia are significantly different (but see pseudepiphallic median process, Figure 17), it is identified here *P. centralis* Desutter-Grandcolas, n. sp. Stridulatory file teeth could not be observed (specimen pinned in the file).

In the same way, one female from the type locality is much smaller than the allotype (compare measurements); it has somewhat different subgenital plate (Figure 19) and copulatory papilla (Figure 21), but this could result from allometric size difference.

Protathra centralis Desutter-Grandcolas, n. sp. could anyway reveal highly variable in size, as observed previously for phalangopsid crickets with the same general appearance (see Desutter-Grandcolas, 1992 for *Phalangopsis longipes* Serville, 1831).

All these specimens have been kept in alcohol, and their coloration is much less contrasted than other specimens.

TABLE 2
Measurements (in mm, mean in parentheses) for *Protathra centralis* Desutter-Grandcolas, n.sp.

	Lpron	wpron	LFW	wFW	LFIII	LTIII
Holotype	3.9	4.5	4.5	5.2	19.7	18.6
Paratypes (n=2)	4.1-4.6	5.3	4.9-5.7	5.6-6.2	20.7-23.4	20.9-22.2
Mean (n=3)	4.2	5	5	5.7	21.3	20.6
Amoa male	3.5	4.1	3.9	4.7	18.2	17.2

	Lpron	wpron	LFIII	LTIII	Lovip
Allotype	4.5	5.2	20.4	20.2	21.5
Additional female	3,9	4,8	17,3	17	18,5

ACKNOWLEDGEMENTS

We thank G. Monteith, Brisbane Museum, for the loan of New Caledonian crickets, F. Müller (MNHN) for his help during field work, H. Jourdan (IRD Nouméa) for his long lasting collaboration, S. Hugel and D. Rentz for their comments on the manuscript. Field work has been supported by ANR BIONEOCAL (P. Grandcolas) and IRD, Nouméa. Photos of studied specimens were made by G. Lecorvec (MNHN).

REFERENCES

- DESUTTER L. 1987 — Structure et évolution du complexe phallique des Grylloidea (Orthoptera) et classification des genres néotropicaux de Grylloidea. 1ère partie. *Annales de la Société entomologique de France* (n.s.) 23: 213-239.
- DESUTTER-GRANDCOLAS L. 1992 — Les Phalangopsidae de Guyane française (Orthoptères, Grylloidea): systématique, éléments de phylogénie et de biologie. *Bulletin du Muséum national d'Histoire naturelle, Paris*, 4e sér., 14, section A, 1: 93-177.
- DESUTTER-GRANDCOLAS L. 1997a — Le peuplement de grillons (Orthoptères Grylloidea) des sous-bois forestiers du Col d'Amieu (Nouvelle-Calédonie). II. Analyse systématique, in NAJT J. & MATILE L. (eds), *Zoologia Neocaledonica*, vol. 4. *Mémoires du Muséum national d'Histoire naturelle* 171: 137-163.
- DESUTTER-GRANDCOLAS L. 1997b — Le peuplement de grillons (Orthoptères Grylloidea) des sous-bois forestiers du Col d'Amieu (Nouvelle-Calédonie). I. Étude du peuplement. *Zoologia Neocaledonica*, in NAJT J. & MATILE L. (eds), *Zoologia Neocaledonica*, vol. 4. *Mémoires du Muséum national d'Histoire naturelle* 171: 125-135.
- DESUTTER-GRANDCOLAS L. 1997c — Les grillons de Nouvelle-Calédonie (Orthoptères Grylloidea): espèces et données nouvelles, in NAJT J. & MATILE L. (eds), *Zoologia Neocaledonica*, vol. 4. *Mémoires du Muséum national d'Histoire naturelle* 171: 165-177.
- DESUTTER-GRANDCOLAS L. 2002 — The Phalangopsidae (Orthoptera Grylloidea) of New Caledonia, with descriptions of four new species. Systématique et endémisme en Nouvelle-Calédonie, in NAJT J. & GRANDCOLAS P. (eds), *Zoologia Neocaledonica*, vol. 5. *Mémoires du Muséum national d'Histoire naturelle* 187: 103-115.
- DESUTTER-GRANDCOLAS L. 2003 — Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta* 32: 525-561.
- RAGGE D. R. & REYNOLDS W. J. 1998 — The songs of the grasshoppers and crickets of Western Europe. Colchester, England, Harley Books, x + 591 p.
- ROBILLARD T. & DESUTTER-GRANDCOLAS L. 2004 — Phylogeny and the modalities of acoustic diversification in extant Eneopterinae crickets (Insecta, Orthoptera, Grylloidea, Eneopteridae). *Cladistics* 20: 271-293.
- ROBILLARD T., NATTIER R. & DESUTTER-GRANDCOLAS L. 2010 — New species of the New Caledonian endemic genus *Agnotecous* (Orthoptera, Grylloidea, Eneopterinae, Lebinthini). *Zootaxa* 2559: 17-35.
- SPECHT R. 2008 — Avisoft-SASLab version 4.40. Avisoft Bioacoustics, Berlin. Available from <http://www.avisoft.com>.

Three new species and a synonymy in the genus *Nobarnus* (Insecta: Heteroptera: Tingidae)

Éric Guilbert

Muséum national d'Histoire naturelle, Institut de Systématique, Évolution, Biodiversité, ISYEB - UMR 7205 CNRS, UPMC, EPHE, CP 50, 45, rue Buffon, 75005 Paris, France
guilbert@mnhn.fr

ABSTRACT

Three new species of the genus *Nobarnus* Distant are described from New Caledonia, namely *Nobarnus monteithi*, *Nobarnus wanati* and *Nobarnus doboszi*. *Nobarnus kotejai* is synonymized with *Nobarnus signatus*. A key to species is provided.

RÉSUMÉ

Trois nouvelles espèces et une synonymie pour le genre *Nobarnus* (Insectes : Hétéroptères : Tingidae).

Trois nouvelles espèces du genre *Nobarnus* Distant sont décrites de Nouvelle-Calédonie, nommément *Nobarnus monteithi*, *Nobarnus wanati* et *Nobarnus doboszi*. *Nobarnus kotejai* est mis en synonymie avec *Nobarnus signatus*. Une clé de détermination à l'espèce est proposée.

INTRODUCTION

New Caledonian Tingidae include 43 species, of which more than 80% being regionally endemic. Four genera are endemic to New Caledonia: the genus *Corinthus* Distant, grouping two species, the genera *Cephalidiosus* Guilbert and *Nobarnus* Distant, grouping seven and eight species, respectively, and the monotypic genus *Caledoderus* Guilbert. One species is known to occur mainly in Australia, namely *Parada torta* Drake, and two species are known to be widespread, namely *Stephanitis subfasciata* Horvath and *Teleonemia scrupulosa* Drake, the later has been recently introduced in New Caledonia. Most of the species are known to occur in restricted areas. A recent study was made to test hypotheses about the possible causes of diversification of the genera *Cephalidiosus* and *Nobarnus* (Murienne *et al.* 2009). The genus *Nobarnus* Distant 1920, revised by Guilbert (1998), is endemic to New Caledonia and currently consists of eight species. These are *N. signatus*

(Distant, 1920), *N. typicus* (Distant, 1920), *N. albiceps* Guilbert, 1998, *N. nigriceps* Guilbert, 1998, *N. pilosus* Guilbert, 1998, *N. quadrispini* Guilbert, 2002, *N. kotejai* Lis, 2006, and *N. picarti* Guilbert, 2008. Recent surveys have uncovered three species of *Nobarnus* new to science, namely *N. monteithi* n. sp., *N. wanati* n. sp. and *N. doboszi* n. sp., and a synonymization. Herein I also describe the instars of several species which exhibit traits that can be used in phylogenetic studies (Guilbert 2004).

MATERIAL AND METHODS

Specimens were examined with a Leica MZ16 binocular microscope. They are deposited in the following institutions; Muséum national d'Histoire naturelle (MNHN), Queensland Museum of Natural History, Australia (QMNH), and Upper Silesian Museum, Poland (USMP). All measurements are in millimeters.

SYSTEMATIC PART

Family TINGIDAE Laporte, 1833

Genus ***NOBARNUS*** Distant, 1920

Nobarnus Distant, 1920: 156.

Type species. *N. typicus* Distant 1920: p. 156. Carded specimen, holotype Male, BMNH, Mont Arago, New Caledonia.

DIAGNOSIS — Head short; bucculae with two or three rows of small areolae; antennae slender, finely pilose, first segment slightly shorter than fourth, second the shortest and third the longest; legs slender. Pronotum wide, tricarinate, the carinae straight; paranota narrow, hyaline, with a row of areolae at most; hemelytra broad, widened strongly at base; costal area wide, with 4 to 8 areolae widthwise at its widest part, subcostal and discoidal areas with 4-5 rows of areolae, sutural area with 3-4 rows; sutural, subcostal and discoidal areas with smaller areolae at places covering the body at rest, than elsewhere.

IDENTIFICATION KEY TO SPECIES OF *NOBARNUS*

1. Paranota with a single basal areola opposite to calli 2
 - Paranota with several areola 3
2. Costal area 6 to 7 areolae wide at widest part *N. nigriceps* Guilbert, 1998
 - Costal area 4 to 5 areolae wide at widest part *N. albiceps* Guilbert, 1998
3. Paranota with a single basal areolae opposite to calli and an outer row of areolae..... 4
 - Paranota with several basal areolae opposite to calli 7
4. Body almost glabrous 5
 - Body densely pilose 6
5. Outer row of paranota with relatively large areolae *N. typicus* Distant, 1920
 - Outer row of paranota with tiny areolae *N. picarti* Guilbert, 2008
6. Sutural area 2 areole wide *N. pilosus* Guilbert, 1998
 - Sutural area 4 to 5 areolae wide *N. signatus* (Distant, 1920)
7. Paranotal narrow, with small areolae opposite to calli *N. monteithi* n. sp.
 - Paranota wide, with large areolae all along 8

8. Head with a median spine *N. wanati* n. sp.
– Head without median spine 9
9. Head with a pair of occipital spines *N. quadrispini* Guilbert, 2002
– Head without occipital spines *N. doboszi* n. sp.

***Nobarnus monteithi* n. sp.**

Figure 1

TYPE MATERIAL — Holotype, New Caledonia, 1M, 20°58'S 165°17'E, 500 m, Pic d'Amoa, north slopes, 26 XI 2003, G. Monteith coll., pyrethrum trunks and logs, MNHN. Paratypes, 1F, 21°11'S 165°18'E, 850 m, Aoupinié, top camp, 23 XI 2001 - 01 II 2002, Burwell and Monteith coll., QMNH; 1F, 22°17'S 166°53'E, 250 m, Pic du Grand Kaori, site 2, 22 XII 2004, Q.M. Party, MV light, QMNH; 3F, 22°04,9'S 166°26,8'E, 700-800 m, Dzumac road (South of Mt Couvélé road), 29 XII 2006, R. Dobosz coll. MNHN (1F) and USMP (2F).

ETYMOLOGY — This species is dedicated to Geoff Monteith (QMNH Queensland Museum) who has provided many specimens of New Caledonian Tingidae for study.

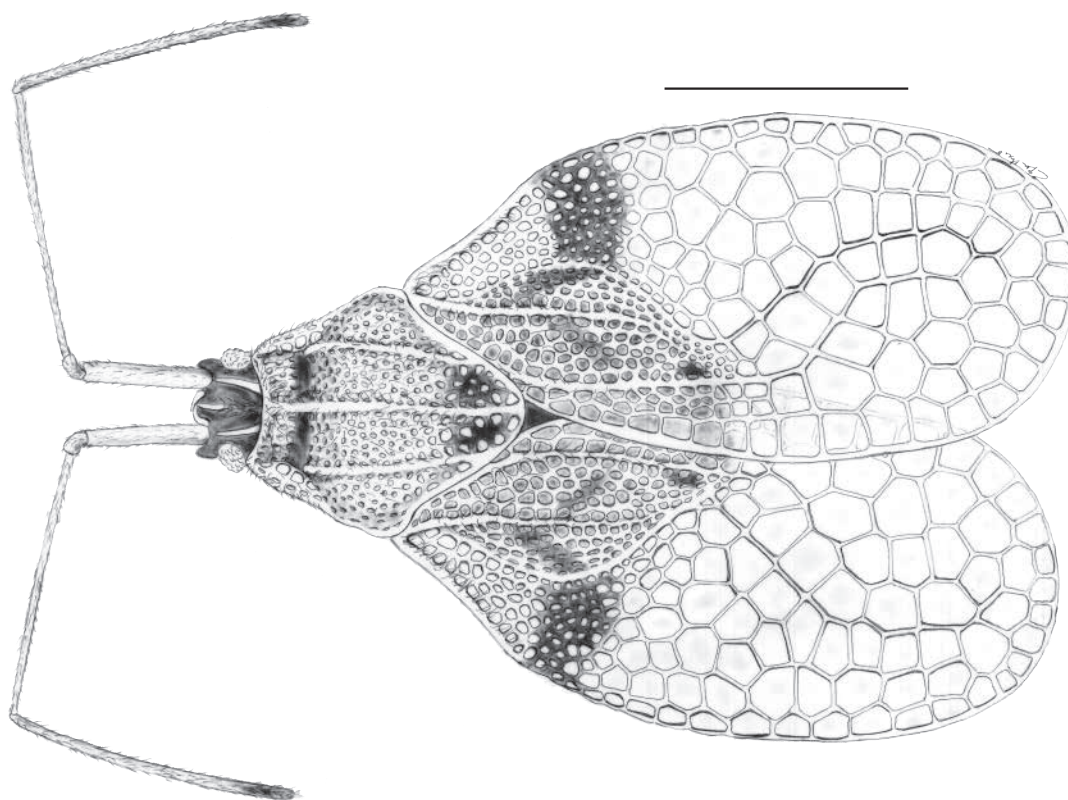


FIGURE 1

Habitus of *Nobarnus monteithi* n. sp. (scale bar = 1 mm)

DESCRIPTION — Body ovate, shiny, glabrous except head and pronotum along carinae, paranota and collar; body whitish to yellowish except tarsi, head, calli, patches on posterior apex of pronotum, top of carinae, patches on hemelytra above abdomen, and a transverse band across the anterior third of hemelytra, which are all brown; body dark brown to black ventrally. Body mean length, 3.88 ± 0.13 ; mean width, 2.68 ± 0.07 ; $n = 6$. Head small and round, armed with five long, slender, appressed spines, frontal and median spines directed downwards, frontal spines stouter than others, in contact at apex, occipital spines directed forwards, apex extending in front of base of median spine; apex of median spine extending in front of base of frontal spines; bucculae wide, with two rows of areolae, closed in front; rostrum short, slightly extending beyond meso-metanotal suture; antennae long and slender, antennal segment measurements: I, 0.612 ± 0.02 ; II, 0.14 ± 0.02 ; III, 1.2 ± 0.08 ; IV, 1.27 ± 0.08 . Pronotum short and wide, strongly gibbose, tricarinate, carinae almost straight and parallel, slightly raised, not areolate, median carinae reaching anterior margin; collar short, with two rows of areolae, anterior margin curved inwards, not raised to form a hood; paranota reduced to a ridge posteriorly, wider opposite to calli, with a row of small subquadrate areolae; posterior process short, rounded at apex; sulcus wide, widening posteriorly, laminae narrow, wider on metanotum, open behind. Legs slender, with second tarsal segment rather stout, almost twice longer than wide, with thick bristle-like hairs on interior face. Hemelytra around 0.6 times longer than abdomen, wide, progressively widening from base to middle length, swollen above abdomen; costal area six areolae wide at widest part, nine areolae wide at the anterior third of hemelytra length, the areolae round and small in the anterior third, large and polygonal in the posterior two thirds of hemelytra length, outer margin bent downwards; Sc vein strongly sinuate; subcostal area strongly bent downwards, five areolae wide, areolae same size and shape as on anterior part of costal area; R+M vein slightly distinct anteriorly, almost indistinct posteriorly; discoidal area five to six areolae wide, areolae same size as on subcostal area; sutural area three areolae wide posteriorly, areolae large and subquadrate as on posterior part of costal area.

COMMENTS — Females have shorter and narrower hemelytra, with a costal area six to seven areolae wide both at the widest part and on anterior third; the subcostal area is five to six areolae wide; the sutural area is three to four areolae wide posteriorly. Brown patches on hemelytra vary in size and shape between specimens. Some specimens have the posterior part of the pronotum, and all hemelytral area above the abdomen, brown.

Nobarnus wanati n. sp.

Figures 2, 3

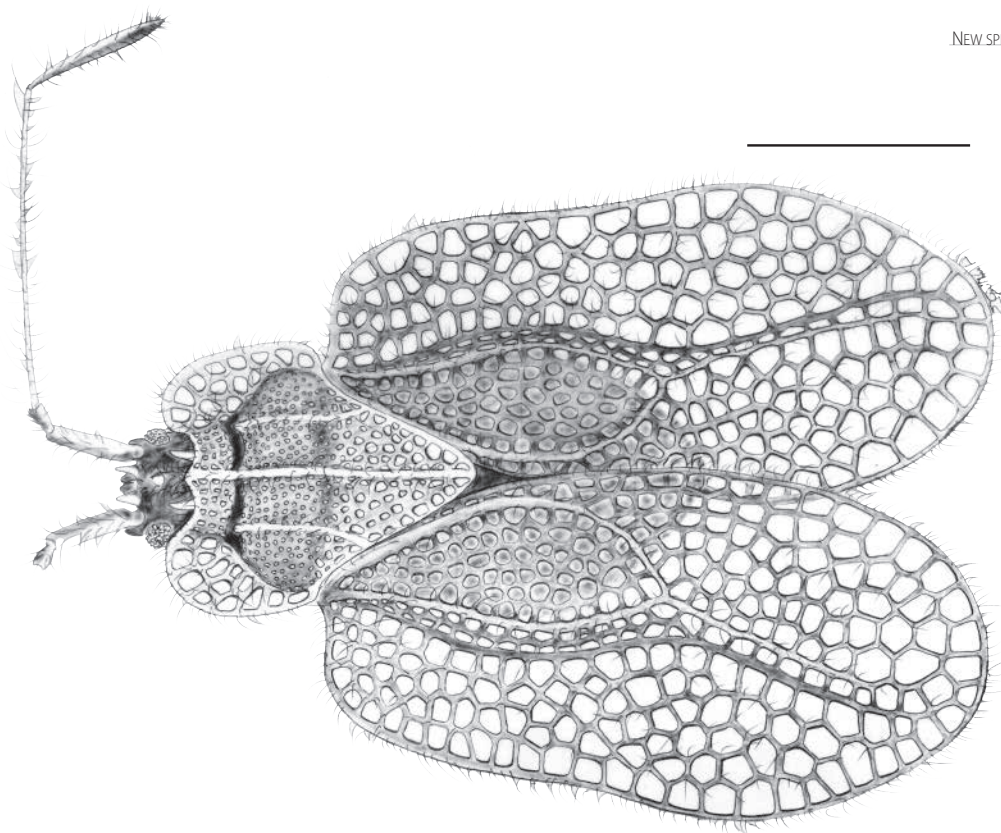
TYPE MATERIAL — Holotype, New Caledonia, 1M, 20°57,2'S 165°17,5'E, 360 m, Pic d'Amoa, forest, 14 I 2007, R. Dobosz & M. Wanat coll. MNHN; Paratype: 1F + 1 nymph (5th instar), same data as holotype, QMNH; 1F, 22°23'S 166°56'E, 150 m, Cap Ndoua, site 1, rainforest, 28 XI 2004, P. Grimbacher coll., beating, QMNH.

ETYMOLOGY — This species is dedicated to Marek Wanat (Museum of Natural History of Wroclaw, Poland) who has provided many specimens of New Caledonian Tingidae for study.

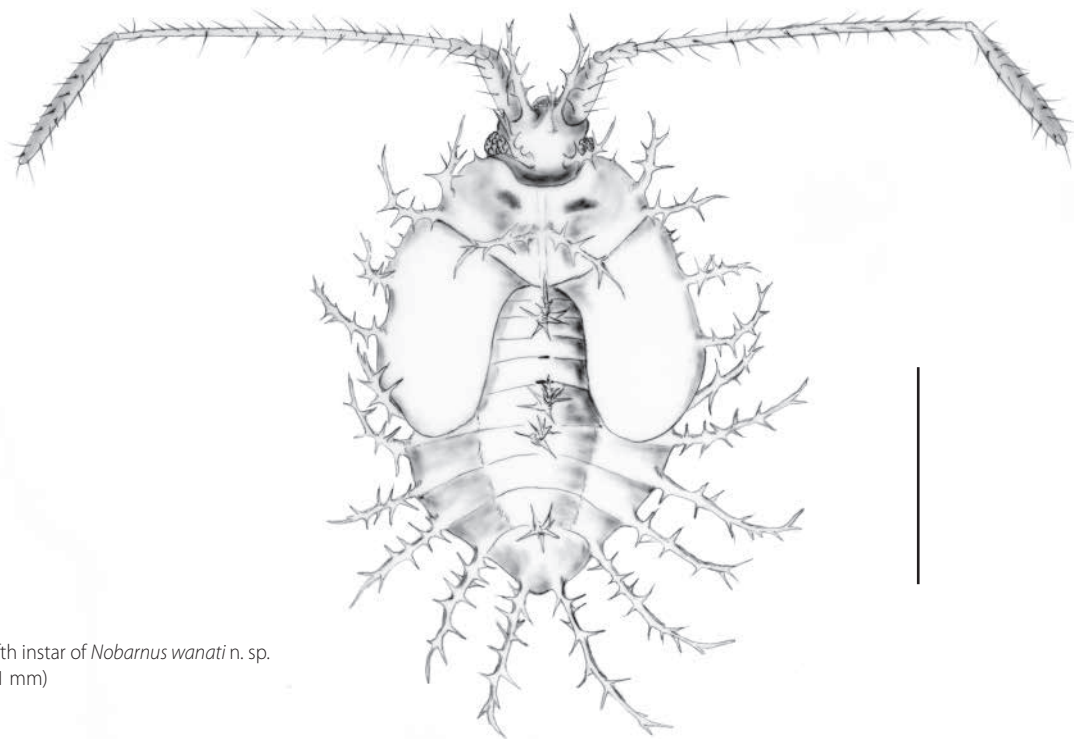
DESCRIPTION — Body shiny, densely pilose; legs, head, and abdomen clear brown, many veinlets on hemelytra darker brown. Body mean length, 3.89 ± 0.12 ; mean width, 2.79 ± 0.10 , $n=3$.

Head short and wide, armed with five short, stout, erect spines; bucculae narrow, with two rows of areolae, open and not in contact in front; rostrum short, reaching middle of metanotum; antennae long and slender, antennal segment measurements: I, 0.43 ± 0.04 ; II, 0.17 ± 0.01 ; III, 1.44 ± 0.08 ; IV, 0.57 ± 0.12 .

Pronotum wide, gibbose in the middle, tricarinate; carinae distinct, subparallel, with a row of small areolae, lateral carinae slightly diverging posteriorly, median carina reaching anterior margin; collar three areolae wide, slightly elevated in middle and extended forwards where median carina reach anterior margin, anterior margin curved inwards; paranota developed

**FIGURE 2**

Habitus of adult of *Nobarnus wanati* n. sp. (scale bar = 1 mm)

**FIGURE 3**

Habitus of fifth instar of *Nobarnus wanati* n. sp.
(scale bar = 1 mm)

from humeri to anterior margin, with an outer row of areolae opposite humeri, then two to three areolae wide opposite calli, outer areolae moderately large, inner areolae smaller; pronotal posterior process short, angulate posteriorly, however not sharply; rostral channel wide, slightly wider posteriorly and open beyond, laminae narrow, with a row of small areolae.

Legs slender, with second tarsal segment twice as long as wide, with thick bristle-like hairs on inferior face.

Hemelytra wide, 0.6 time longer than abdomen and extending beyond, widening sharply at base, major veins distinct; costal area wide, five to six areolae wide at widest part, areolae moderately large and polygonal; Sc vein moderately sinuate; subcostal area bent downwards, biseriate, areolae same size and shape as costal area; discoidal area slightly longer than half the length of hemelytra, six areolae wide, areolae smaller than on costal and subcostal areas; junction of R+M and Cu slightly raised; sutural area wide, six areolae wide, areolae same size and shape as costal and subcostal areas.

DESCRIPTION OF FIFTH INSTAR — Body uniformly yellowish to clear brown, shiny, glabrous except pronotum, legs and antennae sparsely covered with long setae, setae located along posterior margin on pronotum; dorsum covered with minute white pedunculate processes, also with long slender and spiny tubercles, the latter tubercles straight, erect, with slender spiny ramifications all along tubercle length, length of tubercles 0.58 to 1.00. Body length, 2.00; width, 1.56.

Head short and wide, armed with five tubercles, a median one, an occipital pair and a frontal pair.

Pronotum wide and short, slightly raised in the median axis, with a pair of tubercles in the middle; across the median axis, lateral margins with two tubercles on the posterior angle; posterior margin angulate in the middle.

Wing pads with two tubercles in the middle of lateral margins.

Metanotum without tubercles.

Abdominal tergites second, fifth, sixth and eighth with a median tubercle in the middle near posterior margin; lateral margins of tergites fourth to ninth with a tubercle on posterior angles.

COMMENTS — The hemelytra of the single male specimen are slightly smaller. The costal area is five areolae wide at widest part, four areolae wide anteriorly. This species differs from other species of the genus by the paranota being much wider, the erect cephalic spines, while they are appressed in all other species, the hemelytral areas plane, while the latter are curved in the other species.

All known nymphs of other *Nobarnus* species do not bear such long and spiny tubercles. This species shows affinities with nymphs of the sister-group genus *Cephalidiosus* due to these tubercles.

Nobarnus doboszi n. sp.

Figures 4, 5

TYPE MATERIAL — Holotype, New Caledonia, 1M, 22°05'33"S 166° 26'892"E, 687 m, Dzumac, site 2, 29 XI 2008, E. Guilbert coll., beating, MNHN. Paratypes, 1M + 1F + 1 nymph (5th instar), same data as holotype, MNHN; 7M + 2F + 4 nymphs (5th instar), 22°07'181" S 166°26'908" E, 400 m, Mont Dzumac, site 1, 29 XI 2008, E. Guilbert coll., beating, MNHN; 4M + 1F + 1 nymph (5th instar), 21°33'873" S 165°46'120" E, 523 m, Table Unio, 02 XII 2008, E. Guilbert coll., beating, MNHN; 1M, 20°33'S 64°46'E, 225 m, Mt Panié, track, 25 IX - 19 XI 2000, Skevington & Burwell coll., Malaise trap, QMNH. 1F, 21°33'S 165°51'E, 300 m, Col d'Amieu, 6KM NNE, rainforest, 13 XI 2000, GB Monteith coll., Pyretrum, trunks & logs, QMNH.

ETYMOLOGY — This species is dedicated to Roland Dobosz (Upper Silesian Museum, Bytom, Poland) who has provided many specimens of New Caledonian Tingidae for study.

DESCRIPTION — Body wide, shiny, densely pilose, uniformly brown, except a transversal band across anterior third of hemelytra, head and body beneath darker brown. Mean body length, 3.25 ± 0.21 ; mean width, 2.31 ± 0.1 , $n = 18$.

Head wide and short, armed with a pair of frontal spines, spines moderately long and slender, some specimens with a vestigial pair of occipital spines, subparallel, curved downwards; bucculae joined in front, narrow, with two rows of areolae; rostrum short, reaching meso-metasternal suture; antennae long and slender, antennal segment measurements: I, 0.45 ± 0.02 ; II, 0.15 ± 0.03 ; III, 1.35 ± 0.14 ; IV, 0.59 ± 0.04 .

Pronotum wide and short, transversally swollen in the middle, tricarinate, carinae distinct for entire length, raised but not areolate; collar wide, with three rows of areolae, curved inwards, not raised to form a hood; paranota wide, with outer rows of large areolae from opposite humeri to anterior margin, with two-three additional inner areolae opposite to calli; posterior process short, posterior margin round and not strongly angulate; rostral sulcus wide and widening posteriorly, open beyond; laminae narrow with a row of small areolae.

Hemelytra 0.6 longer than abdomen beneath and extending beyond abdomen, sharply widened anteriorly; costal area seven areolae wide at widest part, areolae large and polygonal for most of costal area, areolae smaller and round on anterior third where a transverse darker band delineates region; Sc vein sinuate, forming an angle between costal and subcostal area; subcostal area wide on anterior third of hemelytra length, four areolae wide, areolae slightly smaller than on posterior part of costal area; R+M vein distinct anteriorly and almost indistinct posteriorly; discoidal area long and narrow, three areolae wide, areolae the same size as subcostal area; sutural area narrow, two areolae wide anteriorly, three areolae wide posteriorly, areolae larger posteriorly, of same size and shape as costal area.

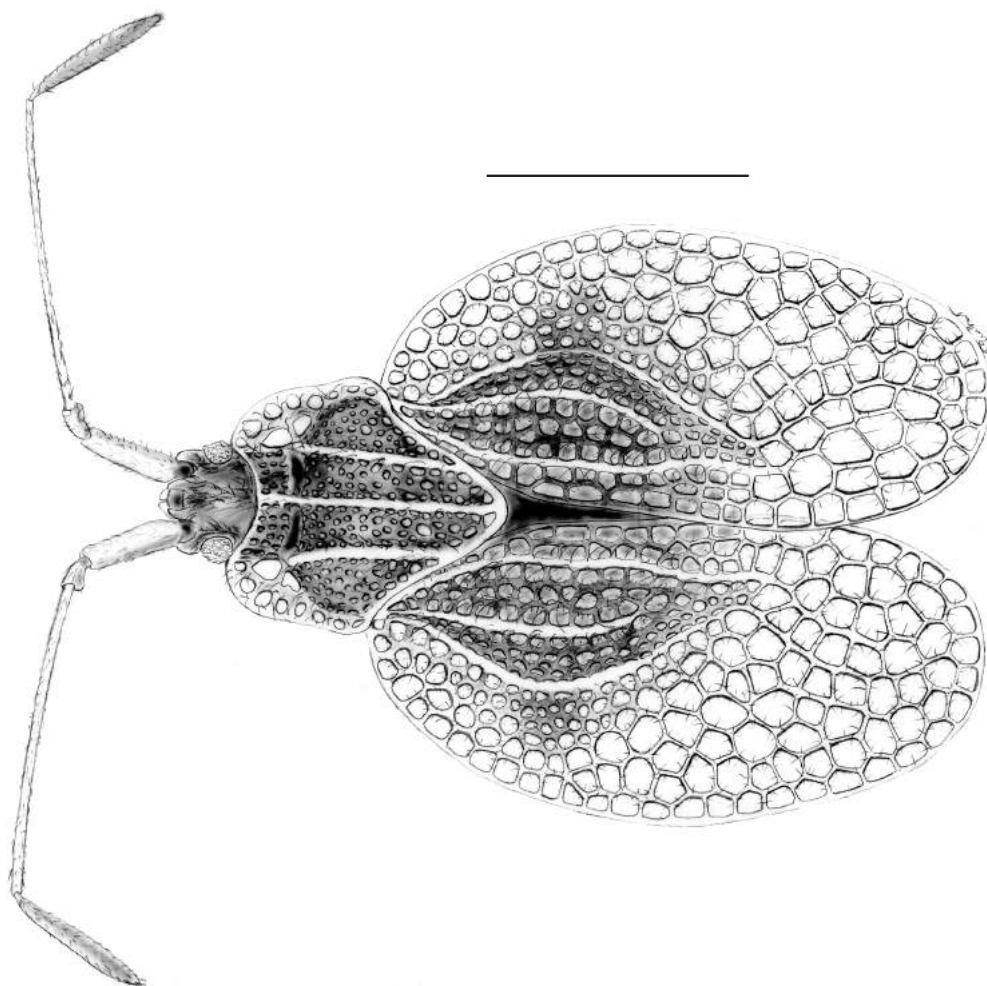


FIGURE 4

Habitus of adult of
Nobarnus doboszi n. sp.
(scale bar = 1 mm)

DESCRIPTION OF FIFTH INSTAR — Body ovate, shiny, glabrous, mostly white. Head, antennae, upper part of collar, two transverse bands on anterior part of wing pads, median part of metanotum, first, second abdominal segments, edges of scent gland orifices, longitudinal band and protuberances of ninth abdominal tergites brown to black. Body (without protuberances) mean length, 1.97 ± 0.21 ; mean width, 1.31 ± 0.12 , $n = 6$.

Head short and wide, armed with five cephalic spines; frontal pair long (0.20), slender and spiny, erected, with small spiny ramifications; median spine short, slender, without ramifications, appressed and directed forwards; occipital pair short, spiny, erected, with two-three minute, spiny ramifications; antenniferous processes rather long and spiny, with small, short protuberances like ramifications on cephalic spines, antennae long and slender, covered with minute, spiny protuberances the same size and shape as on antenniferous processes and cephalic spines; clypeus also with same protuberances.

Pronotum wide and short, somewhat flat except collar slightly raised; lateral margins with eight spiny protuberances, horizontally directed, mostly simple and varying in size, anterior one rather short, most posterior spines longer than others, with minute spiny ramifications; posterior margin with minute structures, peduncle-like.

Wing pads wider than pronotum, outer lateral margins with spiny protuberances varying in size, a spine at two-thirds the length of wing pads is the longest, and with several minute, spiny ramifications; posterior and inner lateral margins with several short spiny protuberances.

Metanotum without protuberances.

Abdominal segments slightly swollen in the middle; fourth to ninth visible abdominal segments with a protuberance on each lateral margin, on posterior angle; protuberances rather long (0.20), horizontally directed, with short, spiny ramification.

COMMENTS — This species and *Nobarnus wanati* share the same paranota shape, however the paranota of *N. doboszi* consists of an outer row of areolae and two large inner areolae opposite to calli, while the paranota of *N. wanati* consists of several areolae organized as an outer row, not as clearly defined as in *N. doboszi*, and more than two inner areolae opposite to calli, the areolae smaller than in *N. doboszi*. *Nobarnus doboszi* is also smaller than *wanati* and shows different hemelytral shape and color patches.

As with most known *Nobarnus* nymphs, the habitus is ovate, with a short and wide head, but protuberances are absent in *N. albiceps* and *N. nigriceps*. The 5th instar of *N. doboszi* varies, however, in general habitus to *N. wanati*, in that the protuberances of the latter are much longer and resemble nymphs of a species of *Cephalidiosus*.



FIGURE 5

Habitus of fifth instar of
Nobarnus doboszi n. sp.
(scale bar = 1 mm)

***Nobarnus signatus* (Distant, 1920)**

Compseuta signata Distant, 1920: 156

Nobarnus signatus – China 1926: 228 – Drake & Davis 1960: 39, fig. 38

Synonym name: *Nobarnus kotejai* Lis, 2006. New junior synonymy.

TAXONOMIC DECISION FOR SYNONYMY — When comparing *N. kotejai* and *N. signatus*, they show some slight variations including the shape of hemelytra, the number of areolae on the costal and sutural areas, and the distinction of the R+M vein. In addition, the type of *N. kotejai* is slightly larger than the type of *N. signatus*. *Nobarnus signatus* shows small, short occipital and frontal spines on the head, which were not mentioned in the redescription of Guilbert (1998). They are deeply concealed by the collar and difficult to see, but these spines vary in size. However, all these variations are not significant enough to warrant the placement of the single specimen of *N. kotejai* as a separate species from *N. signatus*. Furthermore, these two species were found in the same locality (Mont Aoupinié). I propose that the observed differences are within-species variations and herein synonymize *N. kotejai* with *N. signatus*.

DISCUSSION

Cephalidiosus and *Nobarnus* form a monophyletic group, endemic to New Caledonia. They were previously separated by the hemelytral margins bent downwards in *Cephalidiosus*, while they are straight in *Nobarnus* (Murienne *et al.* 2009). The genus *Nobarnus* was found monophyletic on the basis of a greatly widened rostral channel and a single large areola at the base of the paranota (Murienne *et al.* 2009). *Nobarnus monteithi* has the hemelytral margins slightly bent downwards on the anterior half, similar to some species of *Cephalidiosus*. Therefore, the hemelytra margins are not a valid character to separate *Cephalidiosus* from *Nobarnus*. In addition, some of the species of *Nobarnus* described here exhibit several areolae opposite to the calli. The width of the paranota is almost constant along the pronotum in *Cephalidiosus* species, while it varies in *Nobarnus* species. The consistent character in all *Nobarnus* species is that the paranota is wider anteriorly and opposite to the calli. The enlarged rostral channel is, therefore, the only character separating *Nobarnus* from *Cephalidiosus*.

ACKNOWLEDGMENTS

I thank Geof Monteith (Queensland Museum, Australia), Roland Dobosz (Upper Silesian Museum, Poland), Marek Wanat (Wrocław University, Poland), and Christian Mille (IAC, New Caledonia) for having provided many specimens of Tingidae from New Caledonia. I am also grateful to Melinda Moir (University of Western Australia, Australia) and Dominik Chlond (University of Silesia, Poland) for their fruitful comments on the manuscript. This study was partly funded by the program ANR BIONEAL (P. Grandcolas).

REFERENCES

- DISTANT W. L. 1920 — Rhynchota from New Caledonia. *Annual Magazine of Natural History*, ser. 9 6: 143-164.
- GUILBERT É. 1998 — Revision of the New Caledonian genus *Nobarnus* (Hemiptera: Tingidae) with description of three new species. *European Journal of Entomology* 95: 395-406.
- GUILBERT É. 2002 — New data on New Caledonian Tingidae (Hemiptera) with description of new species, in NAJT J. & GRANDCOLAS P. (eds.), *Zoologia neocaledonica*, vol. 5. *Mémoires du Muséum national d'Histoire naturelle* 18: 133-160.
- GUILBERT É. 2004 — Do larvae evolve the same way as adults in Tingidae (Insecta: Heteroptera). *Cladistics* 20: 139-150.
- GUILBERT É. 2008 — New Caledonian Tingidae (Insect: Heteroptera): new species and new records, in GRANDCOLAS P. (ed.) *Zoologia neocaledonica*, vol. 6, *Systématique et endémisme en Nouvelle-Calédonie. Mémoires du Muséum national d'Histoire naturelle* 19: 63-78.
- LIS B. 2006 — New tribal assignment of the genus *Nobarnus* Distant, 1920 (Hemiptera: Tingidae) with a description of *N. kotejai* sp. n. from New Caledonia. *Polish Journal of Entomology* 75: 303-307.
- MURIENNE J., GUILBERT É. & GRANDCOLAS P. 2009 — Species' diversity in the New Caledonian endemic genera *Cephalidiosus* and *Nobarnus* (Insecta: Heteroptera: Tingidae), an approach using phylogeny and species' distribution modelling. *Biological Journal of the Linnean Society* 97: 177-184.

Diversity and distribution of the genus *Rothisilpha* (Dictyoptera, Blattidae) in New Caledonia: Evidence from new microendemic species

Philippe Grandcolas ⁽¹⁾, Romain Nattier ^(1,2), Roseli Pellens ⁽¹⁾ & Frédéric Legendre ⁽¹⁾

⁽¹⁾ Muséum national d'Histoire naturelle, Institut de Systématique, Évolution, Biodiversité, ISYEB - UMR 7205 CNRS, UPMC, EPHE, CP 50, 45, rue Buffon, 75005 Paris, France
pg@mnhn.fr

⁽²⁾ UPR 9034 CNRS, Laboratoire Évolution, Génomes et Spéciation, avenue de la Terrasse, BP1, 91198 Gif sur Yvette, France
Université Paris Diderot, Sorbonne Paris Cité, France

ABSTRACT

Five new microendemic species are described in the genus *Rothisilpha* Grandcolas, 1997, providing a more accurate account of its distribution in New Caledonia. The genus appears spatially restricted to a series of forest locations in the central chain, with apparent absence in several undisturbed, rich and well-sampled other mountains.

RÉSUMÉ

Diversité et distribution du genre *Rothisilpha* (Dictyoptera, Blattidae) en Nouvelle-Calédonie : nouvelles espèces microendémiques.

Cinq espèces nouvelles et microendémiques sont décrites du genre *Rothisilpha* Grandcolas, 1997. Ces espèces permettent de mieux définir la distribution du genre en Nouvelle-Calédonie. Celle-ci reste restreinte à une série de localités forestières dans la chaîne centrale, avec une absence apparente dans d'autres montagnes pourtant non-perturbées, riches et bien échantillonnées.

INTRODUCTION

The island New Caledonia harbors a conspicuous fauna of Blattidae cockroaches that has been recently discovered (Grandcolas 1997; Murienne 2006). This fauna is large and diverse, especially when compared to other faunas of the Australasian region. In this respect, it looks more diverse than the Blattidae fauna of New Zealand, which is yet a much bigger island (Johns 1966; Chinn & Gemmel 2004), even if it is not as large as the fauna of Australia (MacKerras 1968 and therein; Roth 1991). Until recently, the Blattidae of New Caledonia were poorly known with only a few species described by Chopard (1924) and placed at that time in the genus *Cutilia* Stål, 1877 (but see Princis 1974) or by Roth (1987) in the Australian and New Caledonian genus *Tryonicus* Shaw, 1925. Since twenty years, several endemic monophyletic genera with divergent morphologies and ecologies have been collected and described, including many new species distributed all over the main island (Grandcolas 1997; Grandcolas *et al.* 2002; Murienne *et al.* 2005, 2008 a, b; Pellens 2004).

Among these recently described New Caledonian genera, *Rothisilpha* Grandcolas, 1997 was erected to include three well-characterized species collected in 1994 and which were previously unknown (Chopard 1924; Princis 1974; Roth 1987). These microendemic species were found in three distant locations – Rivière Bleue in the South, Col d'Amieu in the center, Aoupinié in the North – but were absent from other locations visited at that time and whose fauna was well known from many previous natural history studies (*e.g.*, Monts Koghis, Mont Do, Mont Mou). These restricted and apparently disjunct species distributions could have been considered peculiar by comparison with other blattid genera or even with other well-studied insects (*e.g.*, Desutter-Grandcolas & Robillard 2006; Nattier *et al.* 2012, 2014) but they were not interpreted at that time, in expectation of more data. Additional field sampling has now been done. We can describe several new species and propose a more accurate account of species diversity and distribution within the genus.

MATERIAL AND METHODS

Specimens were collected during five field trips by P. Grandcolas, F. Legendre & R. Nattier (April 2005, May 2008, May 2009, October 2009 and November 2010). Collecting was performed during the day or at the first hours of the night, looking at any dead organic matter accumulation and habitats where New Caledonian Blattidae and more generally cockroaches have been found (Grandcolas 1994; Grandcolas 1997; Pellens *et al.* 2002; Pellens & Grandcolas 2003). The genitalia were dissected as indicated by Grandcolas (1996) and then studied after clearing in cold KOH. They have been conserved in tubes with glycerin pinned beneath the specimens. Pictures were obtained with a binocular stereomicroscope Leica MZ12 with numerical camera Leica DC200. The nomenclature of male sclerites followed that of Grandcolas (1996), modified from McKittrick (1964). The nomenclature of female sclerites was based on McKittrick (1964). If not specified, all species characters are as defined for the genus in its original description (Grandcolas 1997). The coordinates of each location were registered in the field with a GPS in a WGS 84 coordinate system, and used to map species distribution with the software ArcGIS 10.1.

SYSTEMATIC PART

All the different species considered here have the generic characters defined in Grandcolas (1997) for external and internal morphology. According to the examination of all specimens, some characters usually used to differentiate Blattidae species were here invariable, such as the shape of the supra-anal plate, the coloration of the head or the number and position of spines on the legs. Conversely, the variation between species was well-marked for several characters totally stable within species, such as the shape of sclerites in male and female genitalia and body coloration (especially pronotum). Therefore, descriptions are short but highly discriminating, as shown by the following determination key.

Family BLATTIDAE

Subfamily TRYONICINAE Latreille, 1810

Genus *ROTHISILPHA* Grandcolas, 1997

Type species. *Rothisilpha najtae* Grandcolas, 1997.

***Rothisilpha dzumac* Grandcolas & Legendre, n. sp.**

Figures 2, 9

TYPE MATERIAL — Male holotype, MNHN, Monts Dzumac, 22°03'18,9"S 166°26'55,7"E, 850 m, forêt, 12.V.2009, jour, R. Nattier rec.

TYPE LOCALITY — New Caledonia, Mounts Dzumac, 22°03'18,9"S 166°26'55,7"E, 850 m, forest.

DESCRIPTION — Medium-sized species only known by male. Subgenital plate with a transverse margin between styli.

Male genitalia (Figure 9) very distinctive; sclerite R3v elongated with a mobile and distinct apical process with a spiny tooth; sclerite R3d with a large and curved basis reaching the half of the total width of the genitalia, and then curved and abruptly sharpening toward the apex.

Body coloration brown, except pronotal spots, mouthparts, legs and other appendages tawny yellow. Pronotum (Figure 2) with a continuous lateral yellow band extending straight from the back along the lateral margin and then curved as to reach the eye level on the fore margin. Wings and lateral margins of metanotum with a narrow lateral translucent yellow band in continuation of the pronotal one.

MEASUREMENTS — Body length: ♂: 10 mm. Pronotum length: ♂: 4 mm. Pronotum width: ♂: 4 mm.

ETYMOLOGY — Species named after the type locality.

***Rothisilpha mandjelia* Grandcolas & Legendre, n. sp.**

Figures 4,10,12

TYPE MATERIAL — Male holotype, female allotype, MNHN, Mandjélia, forêt sempervirente, 20°24,102'S 164°31,415'E, 685 m, 30.IV.2005, nuit. P. Grandcolas, J. Murienne, R. Pellens rec. 2 male paratypes, 2 female paratypes, same information as holotype. 1 male paratype, Mandjélia, forêt sempervirente, 20°24'00,7"S 164°31'41,0"E, 680 m, 19.V.2009, nuit, P. Grandcolas rec.

TYPE LOCALITY — New Caledonia, Mandjélia, rain forest, 20°24,102'S 164°31,415'E, 680m.

DESCRIPTION — Small-sized species. Large subgenital plate with a slightly concave margin between styli.

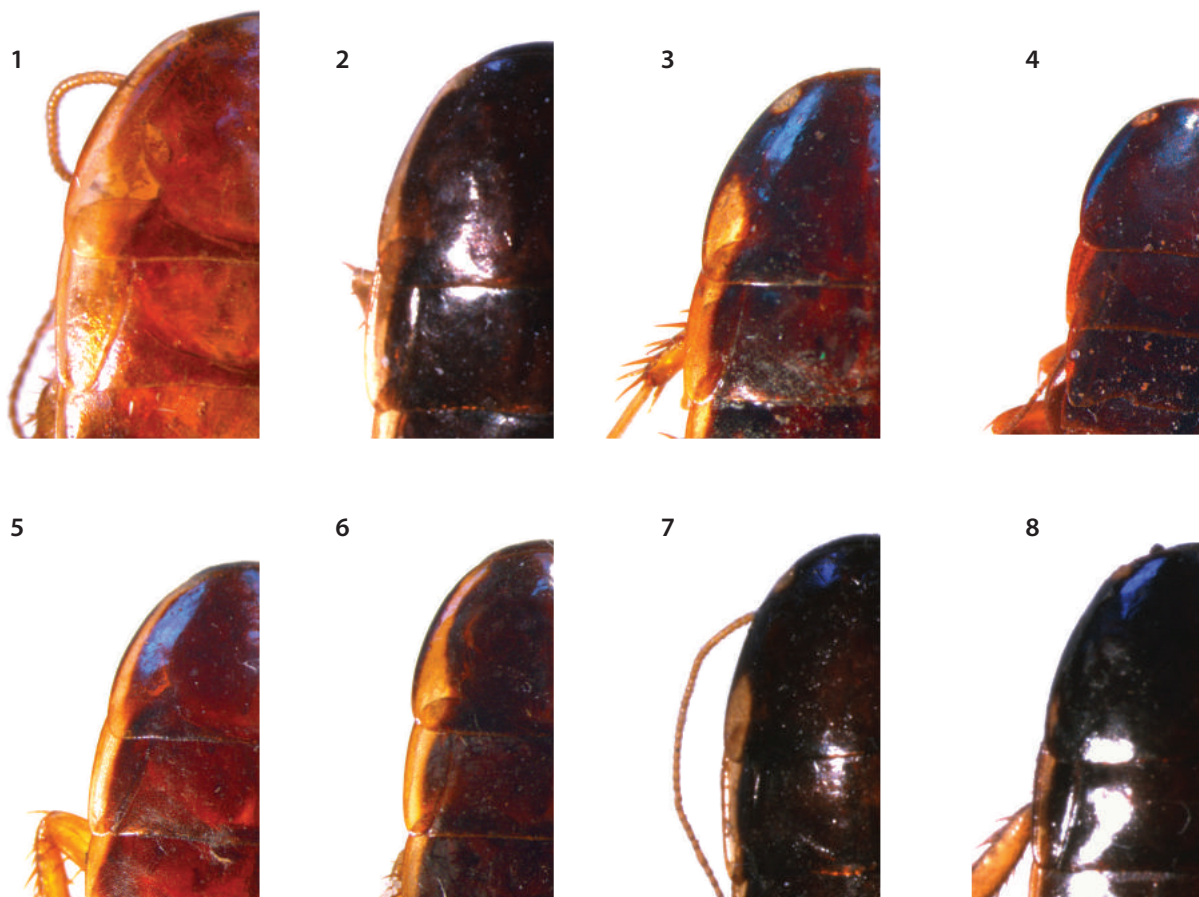
Male genitalia (Figure 10) quite distinctive; sclerite R3v elongated with a subapical dilatation and a dark-sclerotized sharp apex; sclerite R3d robust, cylindrical, directed backward and divided into two apical processes, one blunt and directed inward, and the other sharp and directed backward.

Female genitalia (Figure 12) with very asymmetrical and large first valvifers, the right one protruding inward, the left one slightly folded transversally; basivalvulae also asymmetrical (the right one larger), both well-sclerotized and roughly quadrangular with the inner side curved.

Coloration mostly dark brown; mouthparts, legs and other appendages dark tawny yellow; only one small and yellow rounded pronotal spot at the level of the eye (Figure 4); wings and metanotum dark brown with a very slight lightening on the lateral margin.

MEASUREMENTS — Body length: ♂: 9.5 mm; ♀: 12 mm. Pronotum length: ♂: 3 mm; ♀: 3.7 mm. Pronotum width: ♂: 4 mm; ♀: 5 mm.

ETYMOLOGY — Species named after the type locality.



FIGURES 1-8

Pronotums. **1**, *Rothisilpha bouleti* Grandcolas, 1997. **2**, *Rothisilpha dzumac* Grandcolas & Legendre, n. sp. **3**, *Rothisilpha latreillae* Grandcolas, 1997. **4**, *Rothisilpha mandjelia* Grandcolas & Legendre, n. sp. **5**, *Rothisilpha najtae* Grandcolas, 1997. **6**, *Rothisilpha panie* Grandcolas & Legendre n. sp. **7**, *Rothisilpha touho* Grandcolas & Legendre n. sp. **8**, *Rothisilpha wayem* Grandcolas & Legendre, n. sp. For scales, see the descriptions in the main text.

Rothisilpha panie Grandcolas & Legendre, n. sp.

Figures 6, 11, 13

TYPE MATERIAL — Male holotype, female allotype, MNHN, Mont Panié, Dawenia, 20°32'16,01"S 164°41'51,42"E, 620 m, forêt, 11-15 XI 2010, F. Legendre rec. 1 male, 1 female, paratypes, same information as holotype.

TYPE LOCALITY — New Caledonia, Mount Panié, Dawenia, 20°32'16,01"S 164°41'51,42"E, 620m, forest.

OTHER MATERIAL EXAMINED — 1 male, MNHN, Mont Panié, Wewec, 20°35'17,82"S 164°43'41,25"E, 630 m, forêt, 6-11 XI 2010, F. Legendre rec. 2 female larvae, same information as holotype.

DESCRIPTION — Medium size.

Male genitalia specific (Figure 11); sclerite R3v widened with two sharp and flattened processes; sclerite R3d robust, cylindrical, directed backward and divided into two apical processes, one very short, blunt and directed backward, and the other with a sharp spine and directed outward.

Female genitalia (Figure 13) with asymmetrical large first valvifers with a quadrangular basis, with series of setae on the posterior margin folded on the left, and protruding inward on the right; complex, asymmetrical and large basivalvulae with an inner margin partially thickened, and an outer margin sclerotized and strongly protruding with a sharp apex direct forward, both bearing many small setae inserted at the top of spines.

Coloration rather dark brown, except mouthparts and other appendages; pronotum (Figure 6) with a yellow band extending from the posterior margin until the level of the eye, wider in the posterior third.

MEASUREMENTS — Body length: ♂: 13.5 mm; ♀: 16 mm. Pronotum length: ♂: 3.5 mm; ♀: 4 mm. Pronotum width: ♂: 4.9 mm; ♀: 5 mm.

ETYMOLOGY — Species named after the type locality.

Rothisilpha touho Grandcolas & Legendre, n. sp.

Figures 7, 14

TYPE MATERIAL — Female holotype, 1 female paratype, MNHN, Touho, tour TV, forêt, 20°47'31,2"S 165°13'49,1"E, 270 m, 18.V.2009, jour, R. Nattier rec.

TYPE LOCALITY — Touho, antenne télévision, tour TV, forêt, 20°47'31,2"S 165°13'49,1"E, 270 m.

DESCRIPTION — Medium-sized to small species only known by the female.

Female genitalia (Figure 14) with asymmetrical large first valvifers with a quadrangular basis, smooth except with lines of small setae on the posterior margin; complex, protruding and large basivalvulae with an inner margin curved, protruding and with setae.

Body coloration dark brown, except mouthparts, antennae, palps and legs tawny yellow; pronotum with 4 yellow spots, with on each side a small rounded one at the level of the eye and a large rounded one at the back of the lateral margin (Figure 7); the larger pronotal yellow spot in continuation with a lateral yellow translucent band on the border of the very short wing and the metanotum; smooth and shining cuticle.

MEASUREMENTS — Body length: ♀: 14.5 mm. Pronotum length: ♀: 3.8 mm. Pronotum width: ♀: 4.9 mm.

ETYMOLOGY — Species named after the type locality.

Rothisilpha wayem Grandcolas & Legendre, n. sp.

Figures 8, 15

TYPE MATERIAL — Female holotype, MNHN, Mont Panié, Roches de la Wayem, 20°38'23,56"S 164°52'17,15"E, forêt, 600 m, 1-6 XI 2010, F. Legendre rec. 1 female paratype, same information as holotype.

TYPE LOCALITY — New Caledonia, Mount Panié, Roches de la Wayem, 20°38'56,5"S 164°52'17,15"E, 600 m, forest.

OTHER MATERIAL EXAMINED — 1 female larva, same information as holotype.

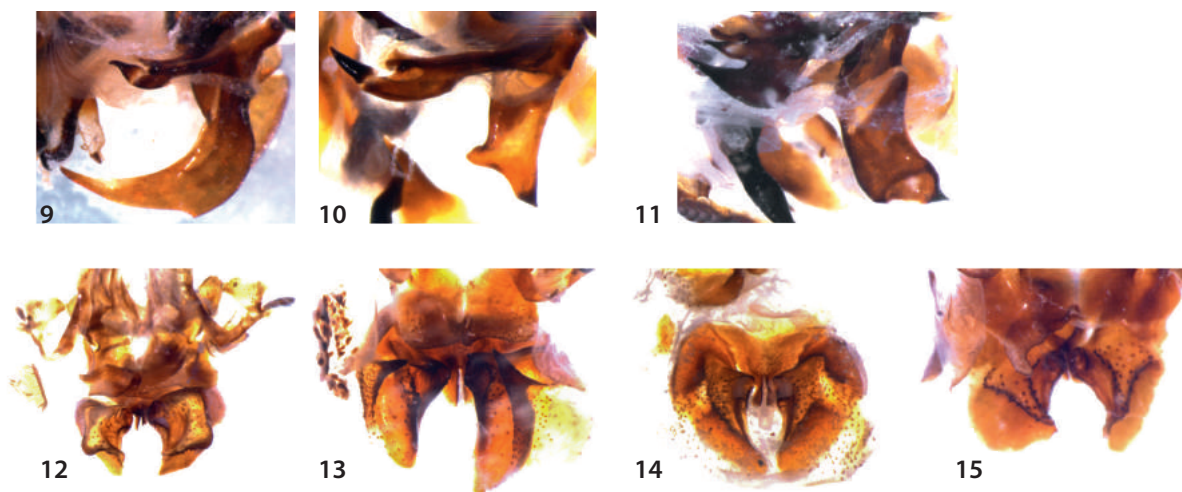
DESCRIPTION — Medium size.

Female genitalia (Figure 15) with asymmetrical large first valvifers with a rounded basis, smooth except one very protruding finger-shaped process formed by the folded posterior margin of the left one; complex and large basivalvulae with an internal margin sclerotized, protruding, sinuous and bearing many small setae inserted at the top of spines.

Coloration dark brown, except mouthparts and other appendages; pronotum (Figure 8) with four small spots, with on each side a smaller one at the level of the eye, and another one slightly larger at the postero-lateral corner in continuation of a narrow translucent yellow band on the border of the wing and metanotum.

MEASUREMENTS — Body length: ♂: 11.5 mm; ♀: 14 mm. Pronotum length: ♂: 3 mm; ♀: 3.8 mm. Pronotum width: ♂: 5 mm; ♀: 5.1 mm.

ETYMOLOGY — Species named after the type locality (also written “Ouaième”).



FIGURES 9-15

9-11. Male genitalia, sclerite R3. 9, *Rothisilpha dzumac* Grandcolas & Legendre, n. sp. 10, *Rothisilpha mandjelia* Grandcolas & Legendre, n. sp. 11, *Rothisilpha panie* Grandcolas & Legendre, n. sp. 12-15. Female genitalia. 12, *Rothisilpha mandjelia* Grandcolas & Legendre, n. sp. 13, *Rothisilpha panie* Grandcolas & Legendre, n. sp. 14, *Rothisilpha touho* Grandcolas & Legendre, n. sp. 15, *Rothisilpha wayem* Grandcolas & Legendre, n. sp.

DETERMINATION KEY

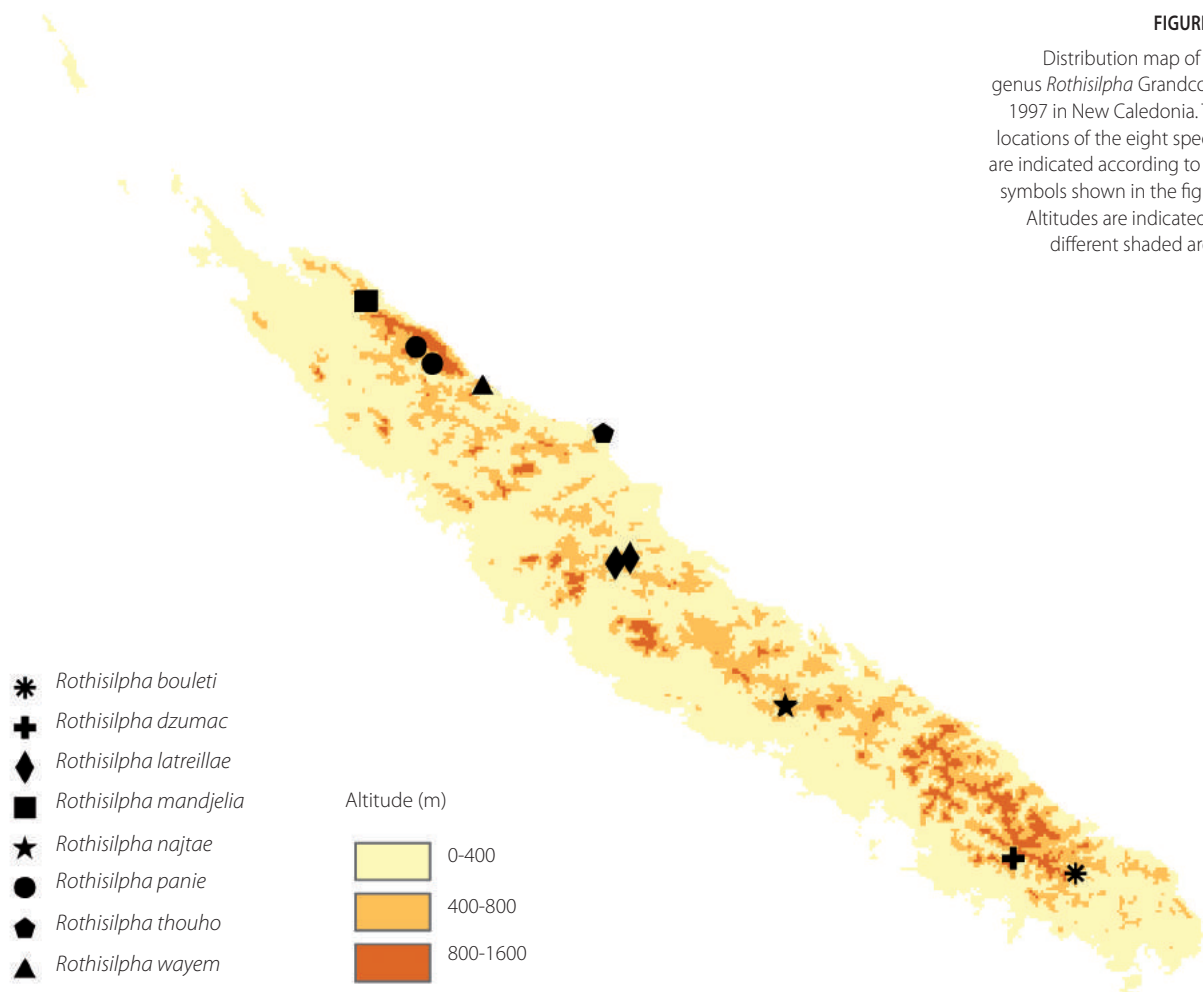
1. Pronotum with only one small yellow spot above the eye (Figure 4). Species small (body length < 9.5 or 12 mm, for males and females respectively) and with coloration dark brown close to black *R. mandjelia* Grandcolas & Legendre, n. sp.
 – Pronotum with one long or two yellow spots. Species larger and brown 2
2. Pronotum with one long yellow spot extending from the posterior margin until above the eye 3
 – Pronotum with two yellow spots, a posterior elongated and an anterior rounded 6
3. Pronotal yellow spot much wider (twice) posteriorly 4
 – Pronotal yellow spot not much wider (less than twice) posteriorly 5
4. Apical posterior part of pronotal yellow spot with parallel margins (Figure 1) *R. bouleti* Grandcolas, 1997
 – Apical posterior part of pronotal yellow spot with the inner margin curved (Figure 6) *R. panie* Grandcolas & Legendre, n. sp.
5. Yellow spot very close to the pronotal lateral margin, making the brown margin reduced to a line; body coloration tawny-brown (Figure 2) *R. dzumac* Grandcolas & Legendre, n. sp.
 – Yellow spot not very close to pronotal lateral margin; body coloration dark brown (Figure 5) *R. najtae* Grandcolas, 1997
6. Posterior yellow spot with the inner margin curved (Figure 3) *R. latreillae* Grandcolas, 1997
 – Posterior yellow spot with the margins parallel (Figure 7) *R. touho* Grandcolas & Legendre, n. sp.

DISCUSSION

According to the present study and to Grandcolas (1997), eight species are now known in the genus *Rothisilpha* Grandcolas, 1997. They all have narrow spatial distribution with absence of sympatry. Each species was found in only a single forested massif although at diverse elevations (between 300–1100 m) (Figure 16). Additional sampling attempts confirmed this trend of microendemism and allopatry, since more individuals of the same species were found again and only in the same original location, with medium abundance (a mean of three–four individuals per sampling session of four hours at night) to very low abundance (one or two individuals per sampling session of four hours).

The new species reduced the geographical disjunction between the three first species originally described, even if each species is still distributed in different and very limited areas. The most remarkable case involves the three species found between Mont Panié and Touho. Although they are only distant from a few kilometers, they are very well-differentiated from a morphological and anatomical point of view. Once again, the origin of such a microendemism can be questioned, given that it cannot be explained by any present or past ecological strong discontinuity (Grandcolas *et al.* 2008). We can only assume that orography (presently with mountains peaking at 1600 m, 138 m, and 982 m) and hydrography (with rivers such as Ouaième or Hienghène) combined with past climatic changes has led to the fragmentation of an ancestral population. Low densities and possible weak dispersal abilities (all species are flightless) could further explain that isolation on different mountains or between rivers has been strong enough to lead to genetic and phenotypic differentiation in spite of the apparent weakness of ecological barriers.

At the level of the whole island, the distribution pattern of the genus is limited to the central chain from the North (Mandjélie) to the South (Rivière Bleue) and with apparent absence from well-sampled side mountains in the southwest, like Mont Mou, Mont Do or Monts Koghis (Figure 16). The genus has not been found either in the Humboldt massif, among the forest patches at the mountain top or basis (Mont Vulcain), but only short stays have been made there (one week or less, respectively, P. Grandcolas, October 2009; R. Pellens & J. Murienné, April 2005), which were possibly not enough to sample the whole local cockroach fauna. Such a global distribution pattern differs from those already known



in the same family of cockroaches (Murienné *et al.* 2005, 2008a) or in other insects (Desutter-Grandcolas & Robillard 2006; Murienné *et al.* 2009; Nattier *et al.* 2012).

Even if different in the details of species distributions, all these cases corroborate a general trend of extreme microendemism within the island (Gasc *et al.* 2013; Pellens & Grandcolas 2010). After the accumulation of field trips and sampling sessions, the characterization of this trend appears very robust since the same microendemic species are always found on the same mountains. The question still pending now is whether microendemic distributions are effectively allopatric or parapatric.

The genus is well characterized as monophyletic and easily identifiable according to several phenotypic features, especially the yellow spots on both sides of the pronotum placed very close to, but actually not on, the margin itself, contrasting with the general brownish coloration of the body (Grandcolas 1997). This coloration character is strongly diversified among the different species, with patterns such as a continuous line, or several spots on the same line or even only one spot. The species are also diverse in size, general body coloration (more or less dark) and genitalia. All individuals were only found in humid forest understory and not in dry sclerophyllous forests or in maquis. The habitat is in the understory at ground level, most often in very tiny cavities formed by piles of dead leaves, twiglets or even by small rocks. Escape behavior can

be characterized as running and digging among items in the litter at very high speed. Much higher abundance and activity were noticed during the night and indicate that the species are nocturnal.

Among the local blattid genera, *Rothisilpha* Grandcolas, 1997 is undoubtedly the most diversified from the point of view of external morphology. However, there is no clear evidence for this specific divergence to be caused by local adaptation, since all species are found in the same microhabitat in apparently similar forested environments and display the same behavior. Further studies could search for more elusive indications of adaptive divergence, for example looking whether the different species show different restricted bioclimatic niches (Murienné *et al.* 2008b, 2009; Nattier *et al.*, 2014). Another functional differentiation could also be searched with the most obviously diversified phenotypic character: the pronotal yellow-colored spots. The position of the anterior spot or part of spot just above the eye suggests the occurrence of an elaborated visual control of light transmittance or motion detection in these insects. Could an adaptive function, for example predator detection, be involved in the diversification of the genus? In this respect, it must be remembered that potential predators in the forest ground litter include small lizards amazingly diversified on the island, whose behavior is varied and could drive the diversification of their potential preys as well (Bauer & Sadlier 2000).

As a matter of conclusion, its distribution pattern and high phenotypic diversity make the genus *Rothisilpha* Grandcolas, 1997 a potential nice model for developing future phylogeographic studies in New Caledonia, and to be compared with previous case studies of other taxa. It should allow testing assumptions about the origin of endemism or even about speciation with adaptive divergence.

ACKNOWLEDGMENTS

Collecting specimens was made according to the permits 60912-1780-2005/JJC, 6024-1446/DRN/ENV and 6034-1414/DRN, provided by Direction des ressources naturelles of Service de l'Environnement de la Province Sud, and Service de l'environnement, Direction du Développement Economique et de l'Environnement, Province Nord. We gratefully thank H. Jourdan (IRD Nouméa) and Christian Mille (IAC) for kindly helping with fieldworks in several occasions, and Edouard Bourguet, Olivier Blight (UMR IMBE, IRD) and Philipp Skipwith (Villanova University) for their help at Mont Panié. Fieldwork was funded by the Programme Pluriformation "Évolution et structure des écosystèmes" (Ministry of Education and Research, Muséum national d'Histoire naturelle), by the grant ANR Biodiversité BIONEOCAL to P. Grandcolas (2008-2011). Sampling in the Mont Panié area in 2010 by F. Legendre was carried out in the framework of a field trip organized by the Institut de Recherche pour le Développement with a grant from DDEE Province Nord and with logistic support from CI and the association Dayu Biik. R. Nattier obtained a Doctorate grant from the Gouvernement de Nouvelle-Calédonie and from the Prévost Fund of the Ecole Doctorale of the Muséum. Maps are produced according to the layers kindly provided by the Direction des Infrastructures, de la Topographie et des Transports Terrestres of the Gouvernement de la Nouvelle-Calédonie under the agreement number CS11-3170-865 to R. Pellens for UMR 7205 CNRS.

REFERENCES

- BAUER A. M. & SADLIER R. A. 2000. — *The Herpetofauna of New Caledonia*. Society for the Study of Amphibians and Reptiles, Ithaca.
- CHINN W. G. & GEMMELL N. J. 2004. — Adaptive radiation within New Zealand endemic species of the cockroach genus *Celatoblatta* Johns (Blattidae): a response to Plio-Pleistocene mountain building and climate change. *Molecular Ecology* 13, 1507-1518.
- CHOPARD L. 1924. — Blattidae de la Nouvelle-Calédonie et des îles Loyalty, in SARRASIN F. & ROUX J. (eds), *Nova Caledonia. Recherches scientifiques en Nouvelle-Calédonie et aux îles Loyalty*, C. W. Kreidel's Verlag, Berlin: 301-336.
- DESUTTER-GRANDCOLAS L. & ROBILLARD T. 2006. — Phylogenetic systematics and evolution of *Agnoteocus* in New Caledonia (Orthoptera: Grylloidea, Eneopteridae). *Systematic Entomology* 31: 65-92.
- GASC A., SUEUR J., PAVOINE S., PELLENS R. & GRANDCOLAS P. 2013. — Biodiversity sampling using a global acoustic approach: contrasting sites with microendemism in New Caledonia. *Plos ONE* 8(5): e65311.
- GRANDCOLAS P. 1994. — Les Blattes de la forêt tropicale de Guyane Française: structure du peuplement (Insecta, Dictyoptera, Blattaria). *Bulletin de la société Zoologique de France* 119: 59-67.

- GRANDCOLAS P. 1996 — The phylogeny of cockroach families: a cladistic appraisal of morpho-anatomical data. *Canadian Journal of Zoology* 74: 508-527.
- GRANDCOLAS P. 1997 — Systématique phylogénétique de la sous-famille des Tryonicinae (Dictyoptera, Blattaria, Blattidae), in NAJT J. & MATILE L. (eds), *Zoologia Neocaledonica*, volume 4. *Mémoires du Muséum national d'Histoire naturelle*, Paris 171: 91-124.
- GRANDCOLAS P., BELLES X., PIULACHS M. D. & D'HAESE C. 2002 — Le genre *Laurasilpha* Grandcolas, 1997: nouvelles espèces, endémisme, séquences d'ARN ribosomique et caractères d'appartenance aux Blattidae (Insectes, Dictyoptères, Blattidae, Tryonicinae), in NAJT J. & GRANDCOLAS P. (eds), *Zoologia Neocaledonica* 5. Systématique et endémisme en Nouvelle-Calédonie. *Mémoires du Muséum national d'Histoire naturelle*, Paris 187: 117-131.
- GRANDCOLAS P., MURIENNE J., ROBILLARD T., DESUTTER-GRANDCOLAS L., JOURDAN H., GUILBERT É. & DEHARVENG L. 2008 — New Caledonia: a very old Darwinian island? *Philosophical Transactions of the Royal Society of London*, B 363: 3309-3317.
- JOHNS P. 1966 — The Cockroaches of New Zealand. *Records of the Canterbury Museum* 8: 93-136.
- MACKERRAS M. J. 1968 — Australian Blattidae (Blattodea). IX. Revision of Polyzosteriinae Tribe Methanini, Tryonicinae, and Blattinae. *Australian Journal of Zoology* 16: 237-331.
- MCKITTRICK F. A. 1964 — Evolutionary study of cockroaches. *Cornell University Agriculture Experiment Station, Memoir* 389: 1-197.
- MURIENNE J. 2006 — *Origine de la biodiversité en Nouvelle-Calédonie. Analyse phylogénétique de l'endémisme chez les Insectes Dictyoptères*. Thèse de Doctorat, Université Pierre et Marie Curie, 341 pp.
- MURIENNE J., GRANDCOLAS P., PIULACHS M. D., BELLES X., D'HAESE C., LEGENDRE F., PELLENS R. & GUILBERT E. 2005 — Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? *Cladistics* 21: 2-7.
- MURIENNE J., GUILBERT E. & GRANDCOLAS P. 2009 — Species diversity in the New Caledonian endemic genera *Cephalidiosus* and *Nobarnus* (Insecta: Heteroptera: Tingidae), an approach using phylogeny and species distribution modeling. *Biological Journal of the Linnean Society* 97: 177-184.
- MURIENNE J., PELLENS R., BUDINOFF R. B., WHEELER W. C. & GRANDCOLAS P. 2008a — Phylogenetic analysis of the cockroach *Laurasilpha* endemic to New Caledonia. Testing competing hypotheses for the diversification of the biota. *Cladistics* 24: 802-812.
- MURIENNE J., PELLENS R. & GRANDCOLAS P. 2008b — Short-range endemism in New Caledonian Insects. New species and distribution in the genus *Laurasilpha* Grandcolas, 1997 (Insecta, Dictyoptera, Blattidae, Tryonicinae), in GRANDCOLAS P. (ed.), *Zoologia Neocaledonica* 6. Biodiversity studies in New Caledonia, *Mémoires du Muséum national d'Histoire naturelle*, Paris 197: 261-271.
- NATTIER R., GRANDCOLAS P., ELIAS M., DESUTTER-GRANDCOLAS L., JOURDAN H., COULOUX A. & ROBILLARD T. 2012 — Secondary sympatry caused by range expansion informs on the dynamics of microendemism in New Caledonia. *Plos ONE* 7: e48047.
- NATTIER R., GRANDCOLAS P., JOURDAN H., COULOUX A., PELLENS R., POULAIN S., ROBILLARD T. 2014 — Climate and soil type together explain the distribution of microendemic species in a biodiversity hotspot. *Plos ONE* 8: e80811.
- PELLENS R., GRANDCOLAS P. & SILVA-NETO I. D. 2002 — A new and independently evolved case of xylophagy and the presence of intestinal flagellates in cockroaches: *Parasphaeria boleiriana* (Dictyoptera, Blaberidae, Zetoborinae) from the remnants of Brazilian Atlantic Forest. *Canadian Journal of Zoology* 80: 350-359.
- PELLENS R. & GRANDCOLAS P. 2003 — Living in Atlantic forest fragments: life habits, behaviour and colony structure of the cockroach *Monastria biguttata* (Dictyoptera, Blaberidae, Blaberinae) in Espírito Santo, Brazil. *Canadian Journal of Zoology* 82: 1929-1937.
- PELLENS R. 2004 — Nouvelles espèces d'*Angustonicus* Grandcolas, 1997 (Insecta, Dictyoptera, Blattaria, Tryonicinae) et endémisme du genre en Nouvelle-Calédonie. *Zoosystema* 26: 307-314.
- PELLENS R. & GRANDCOLAS P. 2010 — Conservation and management of the biodiversity in a hotspot characterized by short range endemism and rarity: the challenge of New Caledonia, in RESCIGNOV. & MALETTA S. (eds), *Biodiversity Hotspots*. Nova Publishers, Hauppauge, NY. pp. 139-151.
- PRINCIS K. 1974 — Ergebnisse der Österreichischen Neukaledonien-Expedition 1965 Blattariae - Schaben. *Annalen des Naturhistorischen Museum Wien*, 78: 513-521.
- ROTH L. M. 1987 — The genus *Tryonicus* Shaw from Australia and New Caledonia (Dictyoptera: Blattidae: Tryonicinae). *Memoirs of the Queensland Museum*, 25: 151-167.
- ROTH L. M. 1991 — Blattodea. Blattaria (Cockroaches), in NAUMANN I. D. & CSIRO (eds), *The Insects of Australia. A text guide for students and researchers*. Volume I, Melbourne University Press, Carlton, Victoria. pp. 320-329.

INDEX TAXONOMIQUE

A

acanthopoma, *Eleotris* 130
Acanthopterus 133-135
 Acari 42
 Achalchinae 209
aculeata, *Hydrometra* 221, 224, 233
aemula, *Sabatinca* 248, 253, 254, 264
aenea, *Sabatinca* 253, 264
aftimacrai, *Parasabatinca* 242
agricolae, *Eurydactylodes* 20
Agrionympha 247, 249, 251, 260
alani, *Oligosoma* 73
alazon, *Leiolopisma* 76
albiceps, *Nobarnus* 290, 296
albofasciatus, *Eugongylus* 72-74
albomaculatus, *Pterogonius* 147-149, 151
albasetosa, *Cyrturella* 212, 214, 218
alticola, *Pterogonius* 147, 149, 151
 Ambassidae 129
amboinensis, *Butis* 130
Amborella 262
amieuensis, *Corindia* 201, 203-206
Amphionotus 162
Anepischetosia 53
 Anguillidae 129, 131
Anisops 219, 220, 226, 229
 Anostomatidae 259, 262
Anotis 53
antiquissima, *Rhyacophila* 242
 Aphelocheiridae 220, 226
Apsilochorema 254, 266
aquilonius, *Caledoniscincus* 73
 Arachnida 42, 276
Aranea 42
argulus, *Microphis* 129
argus, *Scatophagus* 129
armatus, *Hermatobates* 224, 233
artensis, *Prypnus* 146, 148, 150, 151
 Ascalaphidae 267, 268, 276
 Aterpini 133, 134
 Atherinidae 129
atratus, *Stiphodon* 130

atropunctatus, *Caledoniscincus* 20, 28, 43, 123
attiti, *Protogobius* 130, 131
aubei, *Exocelina* 182, 184-186
aurantiaca, *Sabatinca* 253
auratus, *Carassius* 129
aurella, *Micropardalis* 244, 252
aurella, *Sabatinca* 253, 265
Aureopterix 242-244, 252, 254, 257, 259, 263
auriculatus, *Rhacodactylus* 18, 41
auropunctata, *Wasmannia* 15, 22, 28, 30, 43, 92, 99
australicus, *Myrtonymus* 165, 166, 168, 175, 176
australicus, *Ochterus* 226, 227, 236
australis, *Anguilla* 129
australis, *Corindia* 203
australocaledonicus, *Caledoniscincus* 20, 28, 41, 73, 123
Austromartyria 243, 247, 251, 252, 254
Austrovelia 219, 220, 228

B

baaba, *Dierogekko* 16, 18, 25-29
balios, *Sigaloseps* 83, 85-89, 93, 96, 100, 104-110, 113
balteatus, *Redigobius* 129, 131
barbarica, *Sabatinca* 243, 253
Bavayia 14, 18, 28, 43, 65, 111, 116, 125
bellangrensis, *Pindaia* 209, 212, 214-218
 Belontiidae 130
 Belostomatidae 219, 220, 226
 Belostomatinae 226
bergrothi, *Enithares* 227, 238
bergrothi, *Halovelis* 224, 227, 233
bidens, *Acanthopterus* 135-138
bikolanus, *Redigobius* 130
bilunatus, *Copelatus* 181, 182, 184
bimaculata, *Phrynovelia* 186, 224, 225, 232
biocellatus, *Psammogobius* 130
 Blattidae 299, 300, 307, 308
Blechnum 195, 246
bocourti, *Eumeces* 70
bocourti, *Lygosoma* 70
bocourti, *Phoboscincus* 69-74, 76, 77
boreus, *Tropidoscincus* 73

bouleti, *Rothisilpha* 302, 305, 306
brachyurus, *Microphis* 129
breddini, *Hermatobates* 224
brinckii, *Paraphrynoveilia* 222
brownei, *Exocelina* 182, 187
bryophilus, *Pterogonius* 148, 150-152
 Bryophyta 165

C

Caledoderus 289
caledon, *Suhpalacsa* 267-269, 271, 272, 274, 275
caledonica, *Austrovelia* 224, 225, 232
caledonica, *Phrynoveilia* 224, 225, 232
caledonicus, *Myrtonymus* 165, 166, 168-170
caledonicus, *Scirtes* 195-198
Caledoniscincus 41, 43, 62, 78, 115, 116, 118, 119, 123
calliarcha, *Sabatinca* 239, 240, 244, 246, 247, 251, 252, 254, 257, 258, 265
calophylla, *Eucalyptus* 172
Caltathra 278, 279, 281
capricornis, *Corindia* 203
carpio, *Cyprinus* 129
caustica, *Sabatinca* 253, 265
Celatisincus 67, 112
centralis, *Protathra* 277-279, 283, 285-288
 Centrarchidae 129
Cephalidiosus 289, 294, 296, 297, 308
cephalus, *Mugil* 129
 Cerambycidae 42
chalcophanes, *Sabatinca* 253, 254, 258, 265
chloe, *Smilosicyopus* 130, 132
choreutes, *Nannopterix* 241
chrysargyra, *Sabatinca* 239, 240, 242, 244, 246, 252-254, 257, 259, 264
 Chrysidae 42
 Cichlidae 129
cleopatra, *Anisops* 227, 238
Cnetocymatia 226
Coffearhynchus 161
Coleoptera 42, 133, 160, 161, 180, 181, 189, 191, 199, 229, 230
collessi, *Corindia* 203
columnaris, *Araucaria* 138
conditus, *Sigaloseps* 83, 85, 87-89, 92-96, 100, 104, 105, 107, 113
cooloola, *Corindia* 203
Copelatus 184, 186-188
Corindia 201-203, 207, 218
 Corixidae 219, 220, 226, 230, 231
Corynocarpus 259,
crenilabis, *Crenimugil* 129
crinitus, *Anisops* 227, 238
cruentus, *Microphis* 129
Cryptoblepharus 72

Cryptovelia 229
cumini, *Syzygium* 133, 153, 154
 Curculionidae 42, 133, 134, 160, 161, 165, 180
 Curculioninae 134, 146, 165-168
 Curculionoidea 160, 165, 166, 180
Cutilia 300
cylindricus, *Coffearhynchus* 161
cylindricus, *Orthorhinus* 161
Cymatia 226
 Cymatiinae 226
 Cyprinidae 129
cyprinoides, *Hypseleotris* 131
Cyrturella 209, 212-214

D

delobeli, *Sabatinca* 241, 246, 250, 254, 264
demissa, *Sabatinca* 244, 248, 250, 253, 264
deplanchei, *Lygosoma* 86-88
deplanchei, *Sigaloseps* 65, 73, 79-83, 85-96, 101, 104, 105, 107, 112
 Diaprepocoridae 220, 226, 228
 Dicotyledons 165
Dictyoptera 299, 307, 308
Dierogekko 13-15, 17, 19, 23-25, 28-30, 32
 Dilleniaceae 135, 145
 Diplodactylidae 13, 14, 30, 32, 43, 65, 70, 110, 125, 261
 Diptera 201, 203, 207, 209, 218
discoidalis, *Exochomoscirtes* 195
dispersia, *Pindaia* 209-212, 214-217
diversicolor, *Eucalyptus* 172
doboszi, *Nobarnus* 289-291, 294-296
 Dolichopodidae 201, 202, 207, 209, 210, 213, 214, 218
doroxena, *Micropardalis* 244
doroxena, *Sabatinca* 246-248, 253, 265
douei, *Amphionotus* 162, 163
Dracophyllum 133
dufourii, *Ochterus* 221, 226, 237
dufourii, *Pelgonus* 221, 237
 Dytiscidae 181-183, 189, 229
dzumac, *Rothisilpha* 301, 302, 304-306

E-F

ebenus, *Scirtes* 197, 198
 Eleotridae 130, 131
Emoia 36, 72, 78
Enithares 219, 220, 226, 228, 230
enoggera, *Pindaia* 209, 212, 214, 216-218
 Entiminae 133, 134, 146
 Epacridaceae 139
Epimartyria 243, 260-262, 265
 Ericaceae 133, 135, 139

Erirhinini 165-168
eucalypti, *Myrtonymus* 165, 168, 172, 173, 176
Eucalyptus 172, 217, 218
 Eugnomini 133, 134
Eugongylus 34, 36, 37, 52, 53, 69-72, 74, 76-78, 86, 115, 116, 118
Eumeces 74, 77, 125
Exocelina 181-186
Exochomoscirtes 199
exos, *Nannoscincus* 47, 49, 57, 58, 63, 67
exulans, *Rattus* 22
Faustiellus 161
Faustius 161
fauveli, *Pterogonius* 148, 151-153
fehlmanni, *Smilosicyopus* 128, 130
ferrugicauda, *Sigaloseps* 83, 85-89, 93, 96, 100, 102-105, 107, 109, 113
festivus, *Caledoniscincus* 41, 73
Fijivelia 226
flaviscuta, *Corindia* 201, 204-206
flaviventris, *Halobates* 224
 Formicidae 30, 42, 43
fossarum gilguy, *Limnogonus* 223, 226, 227, 235,
frenatus, *Hemidactylus* 20, 22, 23
Freycinetia 141
fuligimentus, *Schismatogobius* 130
fusca, *Eleotris* 130
fuscus, *Nannoscincus* 45, 46, 49, 51, 53-55, 58-63, 67, 80

G

Galaxiidae 129, 131
garnieri, *Lygosoma* 70
garnieri, *Phoboscincus* 20, 41, 69-74, 76
garnotii, *Hemidactylus* 20
garrulus, *Nannoscincus* 45-47, 49, 51-53, 57, 58, 67, 80
 Gasteropoda 42
geitaina, *Bavayia* 18
 Gekkonidae 32, 43
Gekkota 13, 14, 30, 43, 110
 Gelastocoridae 219, 220, 225-227, 229
Gelastocoris 226
gelimensis, *Scirtes* 191-194, 197
germanus, *Halobates* 224, 227, 235
 Gerridae 219, 220, 222, 223, 229, 230
 Gerrinae 223, 229
 Gerromorpha 219-224, 227, 229-232
gigantea, *Protathra* 277-285, 287
 Gobiidae 127-132
 Gonipterini 133, 134, 146
Gonipterus 146, 147
gracilipes, *Anoplolepis* 22
gracilis, *Lygosoma* 53, 55
gracilis, *Nannoscincus* 45-47, 49, 51, 52, 55, 56, 58, 63, 64, 67, 68

Graciliscincus 67, 80, 112, 115, 116, 118
graciloides, *Lygosoma* 53, 65
grande, *Oligosoma* 32, 41
grandis, *Eucalyptus* 217
granulosus, *Acanthopterus* 136-138, 143
greeri, *Nannoscincus* 47, 49, 54, 55, 58, 63, 68, 74
Grylloidea 277, 288, 307
guamensis, *Awaous* 130
guilberti, *Rhyacichthys* 130
guineensis, *Madeovelia* 224
 Gymnospermae 165
gyrinoides, *Bunaka* 130

H

haemorrhoidalis, *Copelatus* 184
Halobates 219, 220, 223, 224, 229, 230
 Halobatinae 223, 230
Halovelina 219, 220, 223, 224, 229
 Haloveliinae 223, 229
hanchisteus, *Nannoscincus* 46, 47, 49, 51, 56, 58, 59, 63, 68, 73
haplorhinus, *Caledoniscincus* 20, 28, 73
 Hebridae 219, 220, 224, 229, 230
 Hebrinae 224
Hebrus 219, 220, 224, 228
heighwayi, *Sabatinca* 244, 246, 250, 252, 254, 265
hellerii, *Xiphophorus* 129
 Helotrephidae 220, 226
 Hemiptera 221, 229-231, 260, 297
Hermatobates 219, 220, 224, 229-231
 Hermatobatidae 219, 220, 224, 229, 231
heterocheilos, *Crenimugil* 129
Heterocleptes 224
 Heterocleptinae 224
Heterocorixa 226
 Heterocorixinae 226
 Heteroptera 221, 222, 227, 229-231, 289, 297, 308
Hexonymus 168, 178
Hibbertia 135
hilli, *Halovelina* 224, 227, 234
horvathi, *Mesovelia* 224, 226, 227, 232
 Horvathiniinae 226
humectus, *Nannoscincus* 47, 49, 51, 56, 58, 59, 63, 68
 Hydrobiosidae 242, 262
Hydrometra 219, 220, 224, 228, 230, 231
 Hydrometridae 219, 220, 224, 229, 231
hydroporoides, *Copelatus* 184
 Hymenoptera 30, 42, 43
hyperion, *Anisops* 227, 238
Hypomartyria 247-249, 252, 263
 Hyrcaninae 224

I-K

ianthina, *Sabatinca* 245, 253, 254, 265
illimis, *Glossogobius* 130
incongruella, *Sabatinca* 239, 240, 244-250, 252, 254, 257, 259, 264
inermis, *Acanthopterus* 133, 135, 139, 140
inexpectatus, *Dierogekko* 13-16, 18-23, 25, 28-30
Insecta 42, 180, 191, 229-231, 260, 261, 288, 289, 297, 307, 308
insulanus, *Lethocerus* 226, 227, 236
insularis, *Dierogekko* 18, 25, 28, 29
interrupta, *Agabus* 187
interrupta, *Ambassis* 129
interrupta, *Exocelina* 182, 187
Issikiomartyria 243, 265
jubatus, *Rhynochetus* 221
kaaea, *Lentipes* 130, 132
kaala, *Marmorosphax* 73
kaalaensis, *Dierogekko* 18, 25, 28
kampeni, *Lamnostoma* 129
Kanakysaurus 67, 112
kanalensis, *Gonipterus* 153
kanalensis, *Pterogonius* 133, 148, 153, 154, 156
katherinae, *Halobates* 224, 227, 235
kerzhneri, *Nerthra* 236
koniambo, *Dierogekko* 18, 25, 28
koniambo, *Nannoscincus* 49, 57-60, 63, 64, 68
kotejai, *Nobarnus* 289, 290, 297
kristenseni, *Sabatinca* 246, 247, 250, 254, 258, 264
Kuhliidae 129
Kunzea 169
Kurokopteryx 243, 265

L

Lacertoides 34, 41, 67, 76, 80, 112
lagocephalus, *Sicyopterus* 130, 131
Lanceocercata 259
latreillae, *Rothisilpha* 302, 305, 306
leachianus, *Rhacodactylus* 41
leiaspis, *Microphis* 129
Leiolopisma 43, 65, 76, 77
Lepidoptera 42, 77, 239-242, 244, 260-262
Leptospermum 69
Leptostylis 41, 42
Leptostylis (*Pycnandra*) 42
Lethocerinae 226
Lethocerus 219, 220, 226
lifouensis, *Parendacustes* 278, 279
liliana, *Exocelina* 186, 187
Limnobatodinae 224
Limnogonus 219, 220, 223
Lioscincus 32, 67, 74, 76, 80, 112
liturata, *Paraplea* 227, 237

longipes, *Phalangopsis* 288
Lophomyrtus 169
loyaltiensis, *Xenobates* 224, 234
lubricus, *Juraphilopotamus* 242
lucens, *Hibbertia* 145
lucilia, *Sabatinca* 244, 248, 252, 265
luctuosa, *Gerris* 221, 236
luctuosus, *Limnogonus* 221, 223, 236
lugubris, *Acanthopterus* 140, 141
lugubris, *Lepidodactylus* 28
Lygosoma 53, 55, 65, 70, 78, 111

M

maccoyi, *Lygosoma* 53
macrorhyncha, *Eucalyptus* 176, 178
Macrovelia 222
Macroveliidae 220, 222
maculata, *Exocelina* 182, 187
maculatus, *Xiphophorus* 129
Madeoveliinae 224
madjo, *Bavayia* 18
maior, *Liadotaulius* 242
major, *Corindia* 202, 203
manautei, *Nannoscincus* 47-49, 51, 57, 58, 63
mandjelia, *Rothisilpha* 301, 302, 304-306
marchei, *Hermatobates* 224, 227, 233
margaritacea, *Giuris* 130
marginata, *Kuhlia* 129, 266
mariei, *Anotis* 45, 46, 51, 53, 54, 61
mariei, *Nannoscincus* 45-47, 49, 51, 54, 58-63, 68, 80
marmorata, *Anguilla* 129
marmorata, *Oedodera* 18, 20
marmorata, *Stenopsyche* 266
Marmorosphax 44, 62-67, 78, 109, 111, 112, 116, 125
maruia, *Lioscincus* 32, 44
Medeterinae 201, 202, 209, 210, 212-214
Megachilidae 42
Megacmonotus 268
megastoma, *Anguilla* 129
Megochterus 226
Melaleuca 135, 143
melanosoma, *Eleotris* 130
mele, *Stiphodon* 129-131
melinoptera, *Liza* 129
mertoni, *Mugilogobius* 130
Mesovelia 219, 220, 224, 228, 231
Mesoveliidae 219, 220, 224, 227-231
Mesoveloidea 224
Metrosideros 169, 259, 262
micans, *Aureopterix* 241, 259, 263
microchir, *Moringua* 129
Microdesmidae 130

microlepis, *Tachygyia* 69-72, 74
 Micronectidae 220, 226, 231
Micropardalis 241, 244, 252, 253
 Micropterigidae 239-243, 245, 248, 251, 253, 254, 257, 258, 260-262
Micropterix 239-244, 249, 254, 260-262, 265
micropus, *Mocoa* 55
Microvelia 219, 220, 223, 224, 226
Microvelia (*Pacificovelina*) 224, 228
 Microveliinae 223, 224, 229, 231
millei, *Pterogonius* 133, 148, 154, 156
minor, *Corindia* 203
miops, *Ambassis* 129
Mniovelia 226
 Molytini 139, 161
 Monocotyledons 165
montana, *Marmorosphax* 63, 80
monteithi, *Nobarnus* 289-291, 297
moorei, *Myrtonymus* 165, 166, 168, 176, 177
 Moringuidae 129
mossambicus, *Oreochromis* 129
 Mugilidae 129
mulleri, *Corindia* 201, 203, 205-207
munda, *Kuhlia* 129
 Muraenidae 129
 Myrtaceae 41, 42, 133, 135, 143, 146, 153, 154, 165-168, 172, 178, 262
Myrtastrum 42
 Myrtonymina 165-168, 180
Myrtonymus 166-169, 172, 178

N

najtae, *Rothisilpha* 301, 302, 305, 306
Nannopterix 243, 244, 259
Nannoscincus 43, 45-47, 49-53, 61, 63, 65, 67, 68, 74, 78, 109, 111, 125
Nannoseps 53
 Naucoridae 220, 226
nehoue, *Exocelina* 181-186
nehoueensis, *Dierogekko* 18, 23, 25, 28
nehouensis, *Scirtes* 198
 Nematoda 41, 42
neocaledonicus, *Coffearhynchus* 161
neocaledonicus, *Galaxias* 129
neocaledonicus, *Parioglossus* 130
 Nepidae 220, 226
 Nepomorpha 219-221, 225, 227, 229-232, 236
Nereivelia 231
Nerthra 219, 220, 226, 228
Nesidovelina 226
 Neuroptera 267, 276
ngoyensis, *Uromyrtus* 42

nielsi, *Exocelina* 182, 188
nigriceps, *Nobarnus* 290, 296
nigricornis, *Corindia* 203
nigrofasciolatum, *Lioscincus* 28, 37, 41
nigrofasciolatus, *Lioscincus* 20, 67, 72-74, 76, 112
 Nitidulidae 42
Nobarnus 289, 290, 294, 296, 297, 308
Nothofagus 213, 218
 Notonectidae 219, 220, 226, 229-231
notospilus, *Mugilogobius* 130
novacaledonica, *Rhagovelina* 224, 226, 228, 234
novacaledonicus, *Cryptoblepharus* 20, 28

O

obscura, *Anguilla* 129
occidentalis, *Sarotherodon* 129
occipitalis, *Anisops* 227, 238
oceanica, *Microvelia* (*Pacificovelina*) 226, 227, 234
ocellaris, *Awaous* 130, 131
 Ochteridae 219, 220, 226, 227, 229, 230
Ochterus 219, 220, 226, 228, 229
Oedodera 15, 20
Oligocheta 42
Oligosoma 76
 Ophichthyidae 129
Ophieleotris 130
orestes, *Caledoniscincus* 73
Oribata 42
orientalis, *Lamnostoma* 129
 Orthoptera 262, 277, 288, 307
Orthorhinoides 161
Orthorhinus 161
otagense, *Oligosoma* 41
ouinensis, *Phaeoscincus* 118, 121-124
oxyrhyncus, *Cestraeus* 129

P

Pacificovelina 224, 226, 228, 234
Palaeomicrodes 243
 Pandanaceae 141, 197, 198
panie, *Rothisilpha* 302-306
panope, *Halobates* 224, 235
papua, *Phrynovelia* 222, 225
paradoxus, *Limnobotodes* 224
Paramartyria 243, 265
Paraphrynovelia 222, 229
 Paraphrynoveliidae 220, 222
Paraplea 219, 220, 226
pardalis, *Lacertoides* 31-44, 67, 73, 74, 76, 112
Parendacustes 278

passalota, Sabatinca 253
peckorum, Myrtonymus 165, 166, 168, 172, 174
pectoralis, Trichogaster 130
 Peloridiidae 221, 229-231, 259, 260
penicillatus, Trachodes 134-136, 142, 143
pentecost, Smilosicyopus 129-131
perfecta, Exocelina 182, 188
perrisi, Raymondionymus 166, 180
Phaeoscincus 118-121, 123, 124
 Phalangopsidae 277-279, 288
philippinensis, Phrynovelia 225, 231
Phoboscincus 36, 37, 40, 67, 69-72, 74, 76, 112
Phrynovelia 219, 220, 224, 225, 228
picarti, Nobarnus 290
pidaxa, Rhagovelia 224, 234
pierucciae, Bleheratherina 129
Pilacmonotus 268
pilosus, Nobarnus 290
Pindaia 209, 210, 212-214
pisinnus, Sigaloseps 83, 85-89, 92, 93, 95-97, 99, 100, 104, 106, 107, 113
Planchonella 41, 42
planiceps, Chelon 129
 Pleidae 220, 226
plicatilis, Cestraeus 129
Poecilia 129
 Poeciliidae 129
poellabauerae, Exocelina 182, 188
polyuranodon, Gymnothorax 129
porocephala, Ophiocara 130
porphyrodes, Austromartyria 241, 242, 263
 Potamocoridae 220, 225
poumensis, Dierogekko 13-15, 18-20, 25, 28, 29
Protathra 277-279, 281, 285
protrusa, Stenocorixa 226
Prypnius 150
 Psocoptera 42
 Pteridophyta 165
Pterogonius 133, 146, 147, 150

Q-R

quadrijuga, Sabatinca 253, 254, 265
quadriscipini, Nobarnus 290, 291
queenslandica, Austrovelia 225
rankini, Nannoscincus 47, 49, 55, 58, 63, 68
rattus, Rattus 22, 28
Raymondionymina 165, 166, 168
reginalis, Hexonymus 165, 166, 168, 178, 179
reinhardtii, Anguilla 129
remyi, Exocelina 182, 188
renevieri, Caledoniscincus 73
 Reptilia 31, 43-45, 65, 77-79, 110, 111, 125, 260

reticulate, Poecilia 98
retzii, Microphis 129
Rhagovelia 219, 220, 223, 224, 226, 230, 231, 234
 Rhagoveliinae 223
Rhinaria 150
 Rhyacichthyidae 130, 131
Rhyacophila 242, 265, 266
 Rhyacophilidae 242
 Rhynochetidae 221
Riopa 70
robensis, Corindia 203
robusta, Bavayia 18
Rothisilpha 299-301, 305-307
rufescens, Eugongylus 72, 74
ruficauda, Sigaloseps 79-83, 85-89, 93, 96, 100-102, 104, 105, 107, 109, 110, 113
rupestris, Kuhlia 129
rutilaureus, Stiphodon 130

S

salmoides, Micropterus 129
 Sapotaceae 41-43
sapphirinus, Stiphodon 130-132
sarasini, Sicyopterus 130
 Scatophagidae 129
schuhi, Veliometra 224
 Scincidae 31, 32, 42-46, 65, 66, 70, 77-80, 110, 111, 125, 259, 260
Scirtes 191-193, 195, 197-199
 Scirtidae 191, 192, 195, 199
Scolopterus 134, 142
scrupulosa, Teleonemia 289
semoni, Stiphodon 128, 130
sericeus, Halobates 224, 227, 235
Seychellovelia 225
shonae, Graciliscincus 67, 73, 92, 111, 112
Sicyopterus 131, 132
Sicyopus 131, 132
Sigaloseps 43, 62, 65, 67, 79-89, 93, 96, 99, 100, 102, 105, 109, 111-113, 116, 125
Sigara 219, 220, 230, 237
Sigara (Tropocorixa) 226, 228
signata, Compseuta 297
signatus, Nobarnus 289, 290, 297
similis, Celatiscincus 73
Simiscincus 67, 80, 112, 115, 116, 118
slevenii, Nannoscincus 45-47, 49, 51-53, 55, 58, 63
Smilosicyopus 131, 132
 Sphecidae 42
Squamata 13, 30, 43, 44, 65, 66, 77, 78, 110, 111, 125
Squamicornia 251
starmuehlneri, Microvelia (Pacifcovelia) 234
 Stenocorixinae 226

Stenogobius 131
Stenopsychidae 242
Stiphodon 132
strigosa, *Hydrometra* 224, 226, 227, 233
subfasciata, *Stephanitis* 289
subjecta, *Exocelina* 181, 182, 184
subjectus, *Copelatus* 184
Suhpalacsa 268, 269, 276
Suphalomitus 268
sylviae, *Pterogonius* 147, 155, 156
symmetricus, *Eurydactylodes* 18
Syngnathidae 129
Syzygium 154

T

tabularis, *Pterogonius* 148, 156, 157
Tachygyia 36, 69-72, 74, 76, 77
tadeuszi, *Sigara* (*Tropocorixa*) 226, 227, 237
tardus, *Pterogonius* 148, 157-159
tasmaniensis, *Tasmantrix* 248
Tasmantis 44, 53, 66, 69-71, 74, 78, 111, 125
Tasmantrix 242, 243, 254, 263
telfarii, *Leiolopisma* 73
Tenebrionidae 42
tetragonurus, *Hinulia* 87-89
thomaswhitei, *Dierokekko* 18, 25, 28
Thrypticus 202, 207, 218
Tibicinidae 259
tillieri, *Lioscincus* 32, 43, 67, 73, 80, 112
timorensis, *Cervus* 20
toamensis, *Phaeoscincus* 118
torresiana, *Corindia* 203
torta, *Parada* 289
touho, *Rothisilpha* 302-305
Trachodes 134, 142
trichopoda, *Amborella* 221, 257
trichopterus, *Trichopodus* 129, 130
tristis, *Acanthopterus* 135, 136, 138, 139, 143-145
tristis, *Scolopterus* 143
tristis, *Trachodes* 143

Troglosironidae 231, 259
Tropidoscincus 65, 112
Tropocorixa 226, 228, 237
truncatipala, *Sigara* (*Tropocorixa*) 227, 237
Tryonicinae 300, 308
Tryonicus 300, 308
Tubuaivelia 226
typicus, *Nobarnus* 290

U-V

undulatus, *Amphionotus* 133, 162, 163
Uromyrtus 41, 42
validiclavis, *Bavayia* 14, 30, 43
validiclavis, *Dierokekko* 18, 19, 23, 25, 28
variabilis, *Tropidoscincus* 44, 67, 80, 112
velatus, *Acanthopterus* 135, 136, 145, 146
Veliidae 219, 220, 222, 223, 229, 231
verticalis verticalis, *Trichocorixa* 219, 220, 226, 237
Vietomartyria 243, 261
viettei, *Sabatinca* 242, 246, 248-250, 253, 254, 263
vitiensis, *Pterogonius* 148, 158, 159
vittatus, *Scirtes* 192
vittigera, *Mesovelgia* 224, 226, 227, 232
viviparus, *Kanakysaurus* 20, 67, 112

W-Z

wanati, *Nobarnus* 289-293, 296
wanati, *Pterogonius* 148, 159
wanati, *Scirtes* 197-199
wayem, *Rothisilpha* 302, 304, 306
Winteraceae 245, 247, 261, 262
Xenobates 219, 220, 223, 224
yateiensis, *Stenogobius* 130, 131
Zealandopterix 242, 243, 252, 254, 263
zelandicus, *Myrtonymus* 166-169, 171
zosterophorum, *Sicyopus* 130
Zygogynum 245, 247, 262

RECENTLY PUBLISHED MEMOIRS

- Tome 205 :** Sylvain CHARBONNIER, Alessandro GARASSINO, Günter SCHWEIGERT & Martin SIMPSON (eds) 2013 — A worldwide review of fossil and extant glypheid and lotogastrid lobsters (Crustacea, Decapoda, Glypheoidea). 304 pp. (ISBN: 978-2-85653-706-0) 69 €.
- Tome 204 :** Shane T. AHYONG, Tin-Yam CHAN, Laure CORBARI & Peter K. L. NG (eds) 2013 — Tropical Deep-Sea Benthos, volume 27. 501 pp. (ISBN: 978-2-85653-692-6) 99 €.
- Tome 203 :** Stéphane PEIGNÉ & Sevket SEN (eds) 2012 — Mammifères de Sansan. 709 pp. (ISBN: 978-2-85653-681-0) 119 €.
- Tome 202 :** Tyson R. ROBERTS 2012 — Systematics, Biology, and Distribution of the Species of the Oceanic Oarfish Genus *Regalecus* (Teleostei, Lampridiformes, Regalecidae). 268 pp. (ISBN: 978-2-85653-677-3) 69 €.
- Tome 201 :** Vincent BELS, Adrià CASINOS, John DAVENPORT, Jean-Pierre GASC, Marc Jamon, Michel LAURIN & Sabine RENOUS 2011 — How vertebrates moved onto land. 200 pp. (ISBN: 978-2-85653-667-4) 55 €.
- Tome 200 :** Anselmo PEÑAS & Emilio ROLÁN 2010 — Deep water Pyramidelloidea of the Tropical South Pacific: *Turbonilla* and related genera, in GOFAS Serge (ed.), Tropical Deep-Sea Benthos, volume 26. 436 pp. (ISBN: 978-2-85653-642-1) 89 €.
- Tome 199 :** Sylvain CHARBONNIER 2009 — Le Lagerstätte de la Voulte. Un environnement bathyal au Jurassique. 272 pp. (ISBN : 978-2-85653-632-2) 59 €.
- Tome 198 :** Philippe GRANDCOLAS (ed.) 2009 — Zoologia Neocaledonica 7. Biodiversity studies in New Caledonia. 440 pp. (ISBN : 978-2-85653-618-6) 75 €.
- Tome 197 :** Philippe GRANDCOLAS (ed.) 2008 — Zoologia Neocaledonica 6. Biodiversity studies in New Caledonia. 326 pp. (ISBN : 978-2-85653-605-6) 59 €.
- Tome 196 :** Virginie HÉROS, Robert H. COWIE & Philippe BOUCHET (eds) 2008 — Tropical Deep-Sea Benthos, volume 25. 806 pp. (ISBN: 978-2-85653-614-8) 139 €.

Prix TTC, frais de port en sus.
Prices in Euros, postage not included.

The Mémoires du Muséum publish the eighth volume of the series *Zoologia Neocaledonica*, dealing with the study of the fauna of New Caledonia, one of the «hot spots» of biodiversity in the Southern hemisphere. More than ever, the study of biodiversity in this megadiverse island is a current question. On the one hand, a growing number of molecular phylogenies bring crucial information about the origin and the evolution of local biodiversity. On the other hand, this biodiversity is more and more threatened by multiple landscape uses and its deleterious consequences. In this context, systematic studies like those of *Zoologia Neocaledonica* are strongly needed as both a background and a primary source of knowledge, invaluable for evolutionary studies and land management policies.

This volume comprises 19 contributions bearing on Lizards, Fishes and diverse Insects, with the description of many species new to Science, taking into account more than one hundred taxa from New Caledonia.

Éric **Guilbert** and Tony **Robillard** are Maître de conférences at the Muséum national d'Histoire naturelle and they study respectively systematics and evolution of lace bugs and crickets. Hervé **Jourdan**, Ingénieur de recherche at Institut de Recherche pour le Développement, Nouméa, studies the ecology and evolution of native and invasive species in New Caledonia. Philippe **Grandcolas**, Directeur de recherche CNRS at the Muséum national d'Histoire naturelle, studies the phylogeny and the evolution of insects. He has been in charge of teams, programs and grants devoted to the study of New Caledonian biodiversity.

***L**es Mémoires du Muséum publient le huitième volume de la série *Zoologia Neocaledonica*, consacrée à l'étude de la faune de la Nouvelle-Calédonie, un des « points sensibles » de la biodiversité dans l'hémisphère Sud. Plus que jamais, l'étude de la biodiversité de cette île est d'actualité. D'une part, des études de phylogénies moléculaires en nombre croissant apportent des informations cruciales sur l'origine de la biodiversité locale. D'autre part, cette biodiversité est de plus en plus menacée de disparition, face à l'utilisation du milieu et à ses conséquences. Dans cette situation, les études systématiques des *Zoologia Neocaledonica* apportent à la fois des connaissances fondamentales et une mise en contexte indispensables aux études de biologie de l'évolution et aux politiques d'aménagement.*

Ce volume comprend 19 articles consacrées aux Lézards, Poissons et divers Insectes avec la description de nombreuses espèces nouvelles pour la science, et la prise en compte de plus de 100 taxons en Nouvelle-Calédonie.

*Éric **Guilbert** et Tony **Robillard** sont Maîtres de conférences au Muséum national d'Histoire naturelle, ils étudient respectivement la systématique et l'évolution des punaises dentelières et des grillons. Hervé **Jourdan**, Ingénieur de recherche à l'Institut de Recherche pour le Développement à Nouméa, étudie l'écologie et l'évolution des espèces natives et invasives en Nouvelle-Calédonie. Philippe **Grandcolas**, Directeur de recherche CNRS au Muséum national d'Histoire naturelle, étudie la phylogénie et l'évolution des Insectes. Ses recherches l'ont conduit à assumer la responsabilité de plusieurs structures de recherche dédiées à l'étude de l'origine de la biodiversité en Nouvelle-Calédonie.*

Mémoires du Muséum national d'Histoire naturelle, Tome 206



MUSÉUM
NATIONAL D'HISTOIRE NATURELLE
**PUBLICATIONS
SCIENTIFIQUES**

ISBN: 978-2-85653-707-7

ISSN: 1243-4442

89 € TTC

