Zootaxa 4728 (3): 341–356
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4728.3.3
http://zoobank.org/urn:lsid:zoobank.org:pub:8BA9A4CE-51F3-4948-ABCF-07FB013C163C

A new species of *Cyrtodactylus* Gray (Gekkonidae: Squamata) from Manus Island, and extended description and range extension for *Cyrtodactylus sermowaiensis* (De Rooij)

PAUL M. OLIVER[1,5], RYAN HARTMAN[2], CAMERON D. TURNER[1], TAYLOR A. WILDE[1], CHRISTOPHER C. AUSTIN[3] & STEPHEN J. RICHARDS[4]

[1] *Environmental Futures Research Institute, Griffith University, 170 Kessels Rd, Brisbane, Queensland 4121, and Biodiversity and Geosciences Program, Queensland Museum, South Brisbane, Queensland, 4101 Australia. E-mail: p.oliver@griffith.edu.au*
[2] *Arcadia University, 450 Easton Rd, Glenside, Pennsylvania 19038, USA*
[3] *Department of Biological Sciences, Museum of Natural Science, 119 Foster Hall, Louisiana State University, Baton Rouge, Louisiana 70803-3216, USA*
[4] *South Australian Museum, North Terrace, Adelaide, South Australia 5000 Australia*
[5] *Corresponding author*

Abstract

Systematic investigations of vertebrate faunas from the islands of Melanesia are revealing high levels of endemism, dynamic biogeographic histories, and in some cases surprisingly long evolutionary histories of insularity. The bent-toed geckos in the *Cyrtodactylus sermowaiensis* Group mainly occur in northern New Guinea and nearby islands, however a further isolated population occurs on Manus Island in the Admiralty Archipelago approximately 300 km to the north of New Guinea. Here we first present a review of the genetic diversity, morphological variation and distribution of *Cyrtodactylus sermowaiensis* from northern New Guinea. Genetic structure and distributional records within *Cyrtodactylus sermowaiensis* broadly overlap with underlying Terranes in northern New Guinea, suggesting divergence on former islands that have been obscured by the infill and uplift of sedimentary basins since the late Pleistocene. Based on a combination of genetic and morphological differentiation we then describe the population from Manus Island as a new species, *Cyrtodactylus crustulus* **sp. nov.** This new species emphasises the high biological endemism and conservation significance of the Admiralty Islands, and especially Manus Island.

Keywords: Adelbert Terrane, Admiralty Islands, Central Cordillera, insular endemism, North Papuan Mountains, Sepik Terrane, Sepik River

Introduction

The islands of eastern Melanesia (sometimes termed Northern Melanesia) lie in the South-west Pacific and span from the Admiralty Islands in the west, as far east as the Solomon Islands, or in some interpretations Fiji and Vanuatu (Mayr & Diamond 2001; Lucky & Sarnat 2010). The biota of this region shows high levels of endemism (e.g., Lavery *et al*. 2016), complex and varying biogeographic patterns (Mayr & Diamond 2001; Austin *et al*. 2010), and in some cases long evolutionary histories of insularity (Oliver *et al*. 2018). Within this region, the Admiralty Islands lie just under 300 kilometres north of the large tropical island of New Guinea and a similar distance northwest of the islands of New Britain and New Ireland. The largest of the Admiralty islands, Manus, is home to a distinctive assemblage of endemic or near-endemic vertebrate species, including birds (six) and frogs (five), lizards (four), and rodents (two) (Dutson 2011; Whitmore *et al*. 2015). Many of these endemic taxa have been described relatively recently (Oliver *et al*. 2016; Timm *et al*. 2016), and museum collections and genetic data indicate that additional evolutionarily distinctive lineages remain undescribed (Aplin *et al*. 2015; Richards & Aplin 2015; Tonione *et al*. 2015).

The geckos in the genus *Cyrtodactylus* Gray are the most diverse lineage of geckos in the world (> 250 species) and in Melanesia (> 30 recognised and candidate species) (Tallowin *et al*. 2018). Numerous species from Melanesia

Accepted by A. Bauer: 29 Nov. 2019; published: 23 Jan. 2020

have been described in the last two decades (Kraus & Allison 2006; Rősler *et al*. 2007; Kraus 2007, 2008; Oliver *et al.* 2008, 2012, 2016; Oliver & Richards 2012; Nielsen & Oliver 2017). However, despite their diversity, they appear to be more recent colonists of Melanesia (Oliver *et al*. 2018) and less effective overwater dispersers when compared with several other broadly co-occurring genera of geckos (*Lepidodactylus* Fitzinger, *Gehyra* Gray and *Nactus* Kluge) (Radtkey *et al*. 1995; Zug 2013; Tonione *et al*. 2015). Accordingly, phylogenetic evidence suggests just two major overwater colonisations eastwards of Papua New Guinea (specifically the Solomon Islands) from the New Guinean region (Oliver *et al*. 2017).

A third putative long-distance (> 100 km) overwater dispersal event by *Cyrtodactylus* northwards of the immediate region of New Guinea involves a poorly known population from Manus. These geckos have historically been assigned to *Cyrtodactylus sermowaiensis* (De Rooij 1915), a species that is widespread in the lowlands and hill forests of northern New Guinea. However, recent genetic analyses identified three putative species in the *C. sermowaiensis* Group: true *C. sermowaiensis* from mainland northern New Guinea, and two insular candidate species from Karkar and Manus islands respectively (*C*. sp. Manus and *C*. sp. Karkar; Tallowin *et al*. 2018). Here we take a step towards resolving the diversity of this Group by presenting a summary of morphological, genetic and distributional data for *C. sermowaiensis* and a description of the new taxon from Manus. The much more morphologically distinctive new species from Karkar is being described elsewhere (F. Kraus, pers. comm), and while we mention it in passing, we do not focus on its taxonomy here.

Methods

Sampling—New specimens were collected by hand at night while spotlighting on field trips across the northern provinces of New Guinea between 1991 and 2014, euthanised using standard practices (intraperitoneal and cardiac injection of chlorobutanol), preserved in 10% formalin and stored in 70% ethanol. Liver samples for genetic analysis were taken from all recently collected specimens. The majority of new material has been lodged at the South Australian Museum (SAMA), but additional samples are lodged at the Papua New Guinea National Museum (PNGNM) and the Texas Natural History Museum (TNHM). Sequence data for one specimen that was newly sequenced for this study was accessioned on GenBank. Other genetic data was taken from Tallowin et al. (2018). Additional genetic samples and comparative material (Appendix I) used in this study are held at the following institutions: American Museum of Natural History (AMNH)—New York; Australian Museum (AMS)—Sydney; British Museum of Natural History (BMNH) –London; Museum of Comparative Biology (MCZ)—Harvard University; Bogor Zoology Museum (MZB)—Bogor; Museum Victoria (NMV)—Melbourne; Naturalis (RMNH)—Amsterdam; South Australian Museum (SAMA)—Adelaide; Western Australian Museum (WAM)—Perth; and Museum für Naturkunde (ZMB)—Berlin.

Genetics—Sequence data and alignment protocols for the NADH dehydrogenase subunit 2 gene (*ND2*) followed those presented in Sistrom *et al*. (2009) and Tallowin *et al*. (2018). Our sequence alignment consists of 1029 bp of ND2 data aligned using the MUSCLE algorithm (Edgar 2004), and subsequently checked by eye. Sequences available on GenBank for *Cyrtodactylus adorus* Shea, Couper, Wilmer & Amey (HQ401166) and *Cyrtodactylus novaeguineae* (Schlegel) (JQ820302) were included as outgroups to the *C. sermowaiensis* Group. Phylogenetic trees were estimated using Maximum Likelihood (RAxML v.7.2.8; Stamatakis 2006) analyses implemented on the CIPRES web portal version 3.1 for online phylogenetic analysis. We partitioned the alignment by codon and applied the GTR-CAT model to each partition. We also estimated net genetic divergences (p-distances) within and between taxa in the *C. sermowaiensis* Group using MEGA v. 7 (Kumar *et al*. 2016).

Morphology—Morphometric measurements and abbreviations follow recent work on Melanesian *Cyrtodactylus* (Nielsen & Oliver 2017; Oliver *et al*. 2019). The following measurements were taken post-preservation with digital calipers or string (TL) to the nearest 0.1 mm, with bilateral measures recorded from the left side of the body: snout-vent length (SVL); tail length, as measured with a string, from the posterior edge of the vent to the tip of the tail (TL); total length of original portion of tail (OT); trunk length from posterior edge of axilla to anterior edge of groin with limbs held at right angles (TrK); maximum head width (HW); maximum head height (HH); head length from tip of snout to anterior margin of ear opening (HL); distance from posterior edge of naris to anterior edge of eye (EN) (used as a proxy for snout-length); transverse diameter of orbit (OrB); minimum internarial distance (IN); transverse diameter along longest axis of ear (EAR); forearm length from base of palm to outer edge of elbow flexed at 90 degrees (FA); and hindlimb length from base of heel to outer edge of knee flexed at 90 degrees (HDL).

The following meristic counts were also taken: left and right enlarged supralabials (SUPR), to both the midpoint of the eye and to the rictus; left and right infralabials to rictus (INFR); rows of dorsal tubercles between the ventrolateral folds (not including those on fold itself) at the midpoint of body (DTR); ventral scale rows in a transverse series between ventrolateral folds at midpoint of the body (VENT); the number of subdigital lamellae (LAM), including both the narrow (distal to the inflection of the digit; not including the ungual sheath) and wide lamellae (proximal to the inflection of the joint) under the first and fourth digits of the left manus and pes; and postcloacal tubercles/spurs (PCTUB).

Dorsal bands (not including nuchal band) were counted from the shoulder joints to the vent. When present, less extensive and weaker brown interstitial bands were not included in these counts.

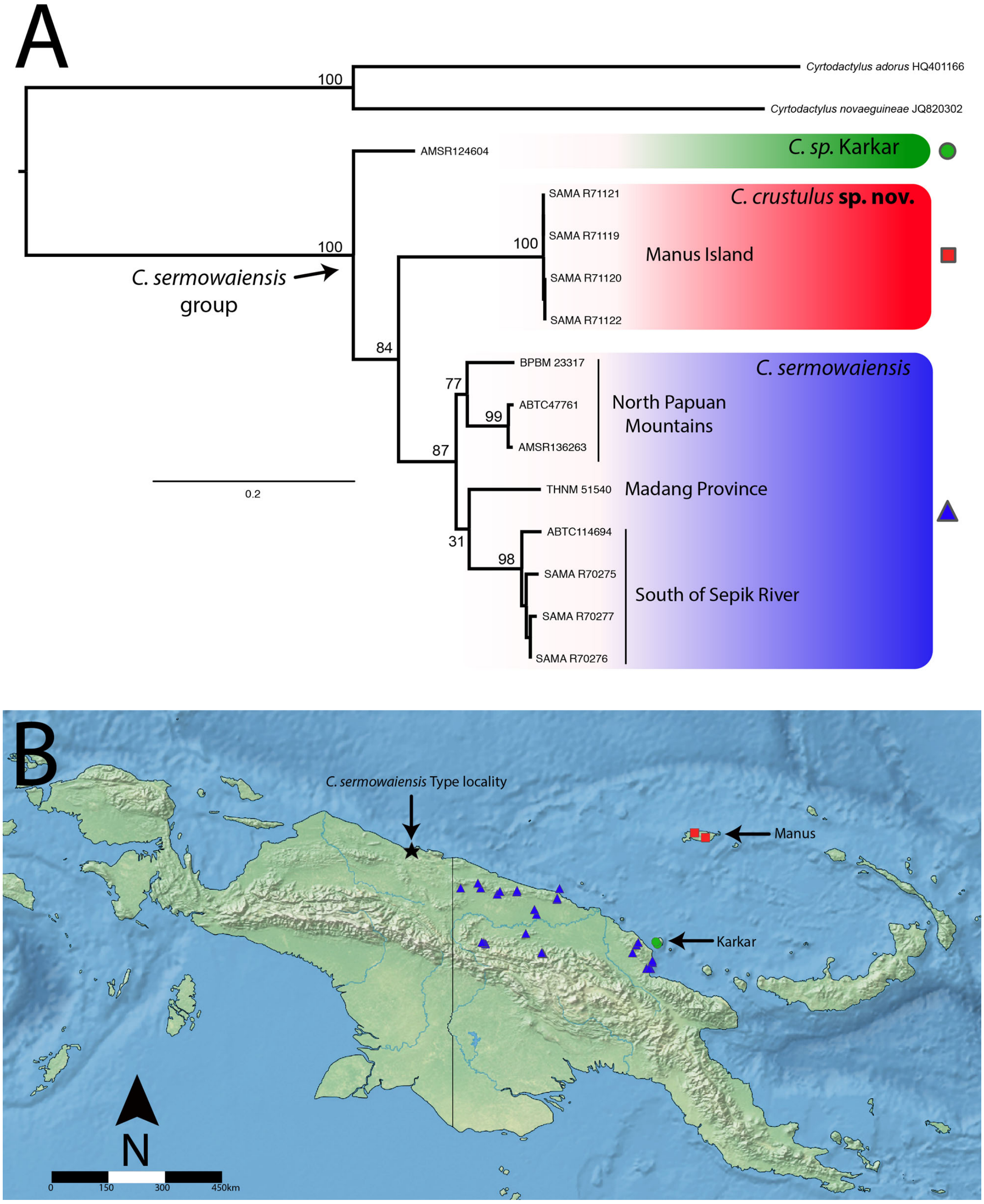

FIGURE 1. A) Phylogenetic relationships and diversity within the *Cyrtodactylus sermowaiensi*s group estimated from 1029 bp of the mitochondrial ND2 gene using Maximum Likelihood. B) Distribution of taxa in the *Cyrtodactylus sermowaiensi*s group based on material lodged in museums. Records of *Cyrtodactylus sermowaiensis* from south of the Sepik River represent southerly range extensions.

Results

Genetics—Phylogenetic analyses identified the same three major lineages within the *C. sermowaiensis* Group as previous analyses (Tallowin *et al*. 2018); *C. sermowaiensis*, *C*. sp. Manus and *C*. sp. Karkar. These three taxa form a strongly supported clade, however the relationships between the three lineages were unresolved (Fig. 1). Mean genetic divergences (uncorrected p-distances) between samples of the three candidate species were always above 10% (0.102–0.124). The two island lineages (Karkar and Manus) were represented by either a single specimen or multiple genetically identical specimens from a single locality. *Cyrtodactylus sermowaiensis* from northern New Guinea, by contrast, showed moderate levels of intraspecific genetic structuring, with three main groups (p-distances > 6%) clustered respectively south of the Sepik River (n = 4), north of the Sepik River and around the Bewani, Torricelli and Prince Alexander Mountains (n=3), and an apparently disjunct population around the Adelbert Mountains in Madang Province (n=1) (Fig. 1).

Morphology—There was overlap between *C. sermowaiensis* and animals from *C*. sp. Manus in most meristic and mensural characters, and both species differed from all other Melanesian *Cyrtodactylus* in the absence of precloacal or femoral pores in males. However in scalation and colour pattern there were a number of consistent differences. Specimens from Manus tended to differ from mainland New Guinean *Cyrtodactylus sermowaiensis* in having larger and more numerous tubercles on the head, body and limbs; more contrasting tubercle colouration on the dorsum; more extensive yellow lateral spotting in life; and distinctive aggregations of pale-brown subcircular markings overlaying the lightly-coloured dorsal regions of the head and neck. These differences are summarised in more detail in the comparisons section for the new species from Manus below.

Systematics

Cyrtodactylus sermowaiensis **(De Rooij, 1915)**

De Rooji's bent–toed gecko
Fig. 2

Material examined for extended description. (n= 21) All from Papua New Guinea. AMS R30797, AMS R30821 East Sepik Province, Passam Village (143.64, -3.70); AMS R129288 East Sepik Province: Jama Village (143.00, -3.966); AMS R129289 East Sepik Province: Pukago Village (142.95, -3.85); AMS R130353–6, AMS R136270 West Sepik Province: Wilbeite Village (142.116, -3.416); AMS R135518 West Sepik Province: Imonda Village (141.116, -3.333); AMS R136263 West Sepik Province: 2Fas Village (141.583, -3.216). SAMA R62653 Madang Province: Kurumbukari: Ramu (-5.58, 145.2); SAMA R62653 Madang Province: Kurumbukari: Ramu (-5.58, 145.20); SAMA R70276–7, SAMA R70279, SAMA R70281–3 border of East Sepik & West Sepik (Sandaun) Provinces: Upper Sepik Region (141.7241, -4.6531); SAMA R70275 West Sepik (Sandaun) Province: Upper Sepik Region (141.7697, -4.6797); SAMA R70278 West Sepik (Sandaun) Province: Upper Sepik Region (141.7698, -4.6800); SAMA R70280 East Sepik Province: Upper Sepik Region (141.6791, -4.6439).

Diagnosis. A species of *Cyrtodactylus* that can be distinguished from all other species of Melanesian *Cyrtodactylus* by the following unique combination of character states: moderate size (adult SVL 78–112 mm); continuous medial row of transversely enlarged subcaudal scales absent; enlarged femoral scales absent; precloacal or femoral pores in males absent; dorsal colouration on body of 5–6 irregular dark-brown dorsal bands or series of blotches (not including nuchal band) alternating with weaker brown interstitial bands; dorsal and lateral tubercles present on proximal and distal segments of all limbs; dorsal tubercles at mid-point of body between lateral skin folds in 16–19 rows; tubercles across supra- and interorbital regions usually <10; majority (>90%) of tubercles within dark-brown dorsal bands also dark brown and not contrasting against surrounding pigmentation; pale yellow lateral spots absent or at most sparse on head and torso; pale regions on dorsal surfaces of neck and posterior head lacking aggregations of subcircular markings; and nuchal band with few or no subcircular indentations along its margins.

Description. A moderately sized gecko (adult SVL 78–112 mm). Head large (HL/SVL 0.24–0.26), moderately wide (HW/SVL 0.17–0.20) and clearly distinct from neck. Snout shorter than broad, rounded in dorsal profile, and truncate in lateral profile. Loreal region slightly inflated, interorbital region and top of snout concave, canthus rostralis rounded and weakly defined. Eye-to-naris distance greater than orbital diameter (EN/ORB 1.07–1.25). Eyes large (OrB/HL 0.25–0.31), pupil vertical, supraciliaries extending from anteroventral to posterodorsal edge of orbit, longest at the anterodorsal margin. Ear opening rhomboidal to circular, bordered by small but distinct dorsal skin fold.

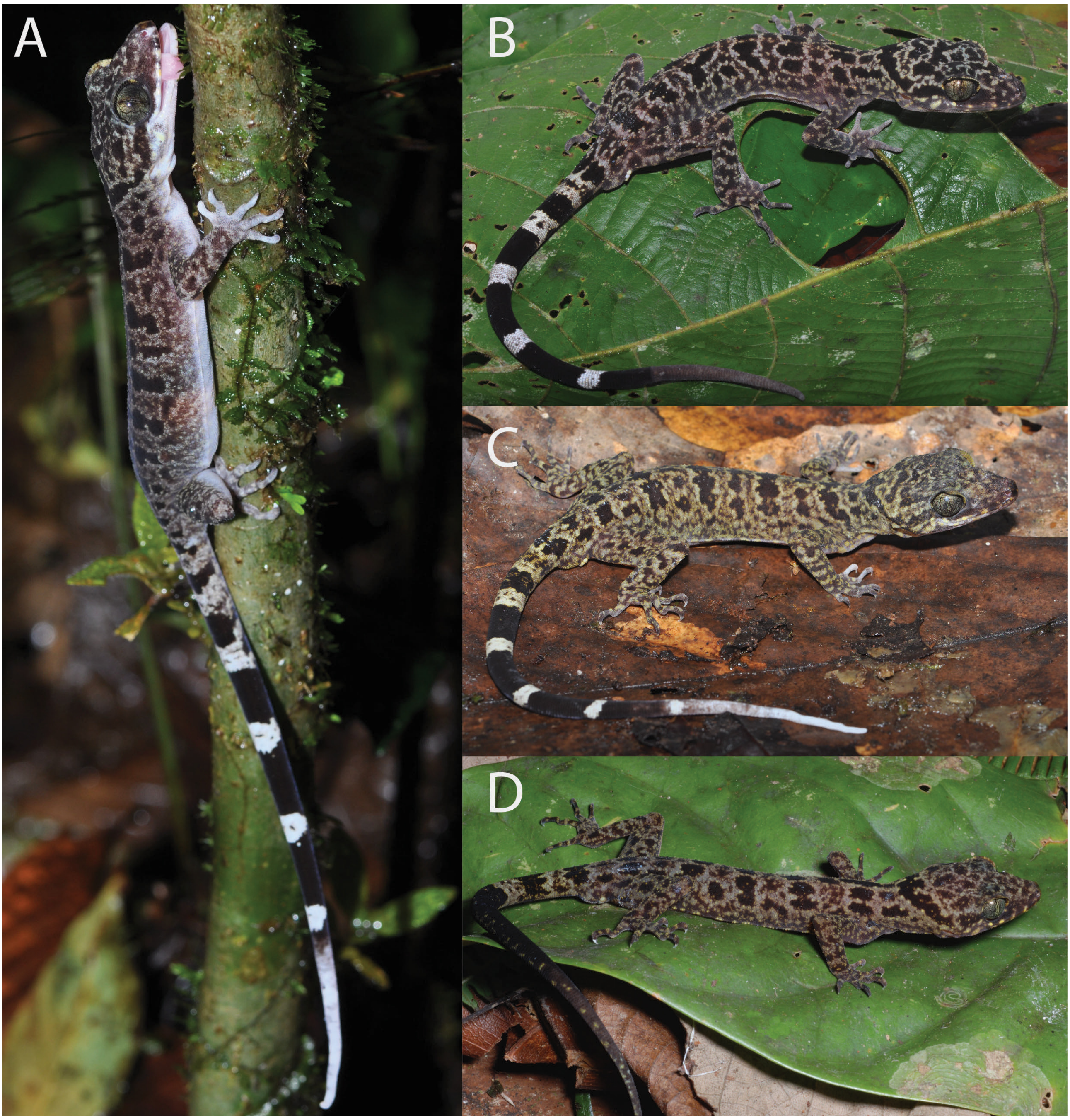

FIGURE 2. *Cyrtodactylus sermowaiensis* in life (all from Papua New Guinea). A) SAMA R70279 photographed in situ at border of East Sepik & West Sepik (Sandaun) Provinces, B) SAMA R70277 at border of East Sepik & West Sepik (Sandaun) Provinces, C) SAMA R70280 from border of East Sepik & West Sepik (Sandaun) Provinces, and D) BPBM35598 Yefehi, Prince Alexander Mountains, East Sepik Province, Papua New Guinea. Photographs A–C Stephen Richards and D Fred Kraus.

Rostral scale subquadrangular with medial cleft and groove at posterodorsal edge, bordered dorsally by two small squarish supranasals and one internasal of similar size to the supranasals. Nares bordered by first supralabial, rostral, supranasal, and 3–6 granular postnasals. Supralabials generally wider than high, 10–12 to rictus of jaw, 8–10 to midpoint of eye. Head scales, temporal scales, and nuchal scales small and granular, in nuchal and temporal regions interspersed with numerous low rounded tubercles approximately two times the width of surrounding scales. Enlarged infralabials 10–13 to rictus of jaw, generally longer than high, becoming narrower anteriorly and posteriorly, bordered by numerous rows of slightly enlarged scales grading into smaller granular scales. Mental triangular, always broader than long, anterior edge rounded. Postmentals always in contact with each other and first infralabial, usually ovoid, large, and extending posteriorly to level of second infralabial.

Body robust (TrK/SVL 0.40–0.52), ventrolateral folds distinct and with tubercles becoming larger posteriorly. Dorsum with 16–19 rows of tubercles, each tubercle up to two times the width of surrounding small granular scales. Ventral scales much larger than dorsal scales, increasing in size medially, arranged in 34–44 rows at midpoint of body. No enlarged row of femoral scales. Femoral and precloacal pores absent in males.

Limbs moderately slender, forelimbs (FA/SVL 0.12–0.15) shorter and less robust than hindlimbs (HDL/SVL 0.15–0.18). Lateral and dorsal surfaces of upper and lower hindlimb with numerous low rounded tubercles up to two times the size of surrounding granular scales. Digits long and well developed, inflected at basal interphalangeal joints; subdigital lamellae smooth, rounded, undivided and expanded proximal to digital inflection (T1 6–8, T4 10–13); narrow distal to digital inflection (T1 6–9, T4 10–13); large recurved claws sheathed by a dorsal and ventral scale.

Original tails thin and moderately long (119–120 mm), with dorsal and lateral grooves, scalation irregular, grading from smaller dorsal scales to larger ventral scales, dorsal tubercles extending <30 mm from tail base, and lateral tubercles extending <20 mm from base, 1–4 postcloacal tubercles on each side. Regrown tails with irregular scalation and lacking tubercles.

In preservative, dorsal and lateral surfaces with ground colouration of greyish-brown to beige on head, neck, torso and limbs. Torso and neck with a series of 5–6 irregular dark-brown transverse dorsal bands or blotches in pairs or quartets, and often further light- to dark-brown interstitial bands and variably dense dark-brown maculations. Nuchal band dark-brown, irregular and tending to extend laterally to posterior edge of orbits. Posterior dorsum of head with 6–8 irregular dark-brown blotches and further maculations of varying extent and density but forming no distinct patterns. Snout, supra- and interorbital regions, and dorsal edge of supracilaries variegated with varying density of dark-brown blotches and smaller maculations. Supracilaries dark-brown in ventral view and tending to have a small number of beige scales. Supralabials barred with dark-brown and beige. Fore- and hindlimbs extensively variegated with light brown to dark brown, often with irregular dark-brown blotches, fingers and toes barred with dark brown and beige. Tubercles across dorsal surface dark brown or beige, tending to match surrounding colouration but with occasional beige tubercles within dark-brown bands. Ventral ground colouration off-white to buff on head and torso, tending to be darker around fore- and hindlimbs, palmar and plantar surfaces with extensive dark-brown ventral maculations. Dorsal surfaces of tail with 6–9 irregular dark-brown bands of greatly varying width separated by narrower regions of beige with scattered dark-brown flecking. Ventral surfaces of tail beige mottled with dark-brown.

Summary of mensural data (in mm) for adults examined (seven males, six females) are as follows (mean, with the range in parentheses): SVL 88.5 (83–98), TrK 41.0 (35.7–48.5), OT (n=2) (119–120); HW 16.7 (14.2–19.3); HL 22.7 (20.1–25.1); HH 10.15 (9.1–11.2); OrB 6.4 (5.5–7.7); FA 12.6 (10.4–14.3); HDL 15.8 (13.8–17.9).
Summary meristic data are as follows: SUPR (to midpoint of eye) 8.8 (8–10); SUPR (rictus of mouth) 11.1 (11–12); INFR 11.4 (10–13); LAMT1 expanded 6.8 (6–8), narrow 7.2 (6–9); LAMT4 expanded 11.6 (10–13), narrow 11.0 (10–13); DTR 18.1 (16–19); VENT 40.4 (34–44); PCTUB 3–4 on each side.

Colouration in life. Based on photographs (Fig. 2) overall pattern in life is broadly consistent with preserved animals. Pale-brownish-yellow spotting and blotching is occasionally present on lateral surfaces of head and torso. Light bands on tail off-white. Iris silvery yellow with extensive irregular dark-brown reticulations.

Comparisons with other species. *Cyrtodactylus sermowaiensis* can be readily distinguished from all other recognised Melanesian *Cyrtodactylus* by the absence of enlarged femoral scales in both sexes and the absence of precloacal or femoral pores in males. The geographic range of *Cyrtodactylus sermowaiensis* only overlaps with a small number of *Cyrtodactylus*. In addition to the characters above, *C. sermowaiensis* can be further distinguished from these overlapping *Cyrtodactylus* species as follows: from *C. equestris* and *C. rex* by its smaller size (max SVL 112 mm *versus* 139 mm and 172 mm respectively), absence of enlarged tubercles on the throat (*versus* present) and dorsal pattern consisting of 5–6 dark-brown transverse bands or blotches (*versus* 2–3 dark to medium-brown bands or blotches); from *C. mimikanus* by lacking transversely widened subcaudals (*versus* present) and dorsal pattern consisting of dark-brown transverse markings with no light border and similarly coloured interstitial bands (*versus* thin dark-brown transverse bands with a light border and no interstitial bands); and from *C. boreoclivus* by lacking transversely widened subcaudals (*versus* present) and in having a light-brown dorsal ground colouration (*versus* mid-brown).

Distribution and Ecology. *Cyrtodactylus sermowaiensis* is known from three distinct geographic clusters. The first cluster occurs from the far northeast of Papua Province, Indonesia (including the type locality at the Sermowai River), through Sandau and East Sepik Provinces. The second cluster occurs around the Adelbert Mountains in Madang Province. The third cluster (based on recent collections by SJR) occurs along the northern versant of the Central Cordillera in Sandau and East Sepik Provinces and is separated from the first cluster by the large Sepik River. It occurs in primary, secondary, and disturbed lowland and hill forest at elevations from near sea-level ~50 m a.s.l. up to nearly 1000 m. a.s.l. It has not been recorded from most of the large floodplain of the Sepik River; however, this area has not been extensively surveyed because it is difficult to access.

This scansorial species is typically observed in low vegetation on trunks of small to large trees and lianas, usually less than two metres above the ground. Unlike other New Guinea *Cyrtodactylus* many specimens have been caught in pitfall traps, suggesting it frequently uses terrestrial microhabitats (F. Kraus, pers. com.). It is sometimes observed perched facing towards the ground, with the head raised above its perch in what may be a hunting posture (Fig. 2A). Three specimens collected in Madang Province were found at night on the rock walls at the mouth of a cave.

IUCN status. *Cyrtodactylus sermowaiensis* is currently listed as Least Concern by the IUCN. Recent surveys have further extended the known distribution of this species into areas with very low human population density, while also confirming that it can occur in moderately disturbed forest habitats close to villages.

Cyrtodactylus crustulus **sp. nov.**
Manus bent-toed gecko
Figs 3–4

Cyrtodactylus sp. 'Manus' Tallowin *et al*. 2018. p. 33

Holotype SAMA R71122 (Field number SJR15091), adult male with original tail, Papua New Guinea, Manus Province, Manus Island, "Yeri camp" (-2.0010, 146.8190), with alcohol-preserved tissue for genetic analysis stored in the Australian Biological Tissues Collection (ABTC 136633), collected by Stephen Richards on 12 October 2014.

Paratypes. (n=4). SAMA R71119 (SJR15075) subadult, SAMA R71120–1 (SJR15076–7), SJR 15092 (to be repatriated to Papua New Guinea) adult males, all with same locality and collector information as holotype, collected between 11–12 October 2014.

Referred material. AMS R130449, Papua New Guinea, Manus Province, Manus Island, Polomou Dpi Station (-2.116, 147.083), collected by Tim Flannery on 16 June 1988.

Diagnosis. A species of *Cyrtodactylus* that can be distinguished from all other species of Papuan *Cyrtodactylus* by the following unique combination of character states: moderate adult size (SVL 93–102 mm); continuous medial row of transversely enlarged subcaudal scales absent; enlarged femoral scales absent; precloacal and femoral pores in males absent; irregularly spaced dark-brown dorsal bands or transverse series of blotches on torso in series of 5–6 (not including nuchal band) with alternating indistinct lighter-brown interstitial bands; dorsal and lateral tubercles present on proximal and distal segments of all limbs; dorsal tubercles at mid-point of body between lateral skin folds in 18–19 rows; tubercles across supra- and interorbital regions usually >10; majority (80–90%) of tubercles within dark-brown dorsal bands light brown and contrasting against surrounding pigmentation; lateral region of head and torso with extensive yellowish spots in life; pale regions on dorsal surfaces of neck and posterior head with indistinct aggregations of light-brown subcircular markings; and nuchal band with regularly scalloped anterior and posterior edges.

Description of holotype. Adult male with original tail, moderate size (SVL 102 mm, TrunkL 45.3 mm) (Fig. 3). Head large (HL/SVL 0.25), moderately wide (HW/SVL 0.19) and clearly distinct from neck. Snout shorter than broad, rounded in dorsal profile and truncate in lateral profile. Loreal region slightly inflated, interorbital region and top of snout concave, canthus rostralis rounded and weakly defined, eye-to-naris distance greater than orbital diameter (EN/OrB 1.21). Eyes large (OrB/HL 0.30), sunken in their sockets, pupil vertical, supraciliaries extending from anteroventral to posterodorsal edge of orbit, longest at the anterodorsal margin. Ear openings rhomboidal, bordered by small but distinct dorsal skin fold.

Rostral scale subquadrangular, wider than high (width 4.5 mm, height 3 mm), bordered posterodorsally by two small squarish supranasals and one internasal similar in size to the supranasals. Nares bordered by first supralabial, rostral, supranasal, and four (left) or three (right) granular postnasals. Supralabials generally wider than high, 12 to rictus of jaw, nine to midpoint of eye. Scales of head—including temporal and nuchal regions - small and granular, interspersed with numerous low rounded tubercles approximately two to three times width of surrounding scales in nuchal and temporal regions. Enlarged infralabials 11, generally longer than high, becoming narrower anteriorly and posteriorly, bordered by numerous rows of slightly enlarged scales grading into smaller granular gular scales. Mental wider than long (width 4.2 mm, height 2.6 mm), anterior edge rounded, concave at point of contact with two postmentals, postmentals large (length 2.8 mm), in contact with each other and the first infralabial on respective sides.

FIGURE 3. *C. crustulus* **sp. nov.** holotype SAMA R71122 in dorsal and ventral views. Scale bar = 10 mm. Photograph. J. Sheridan.

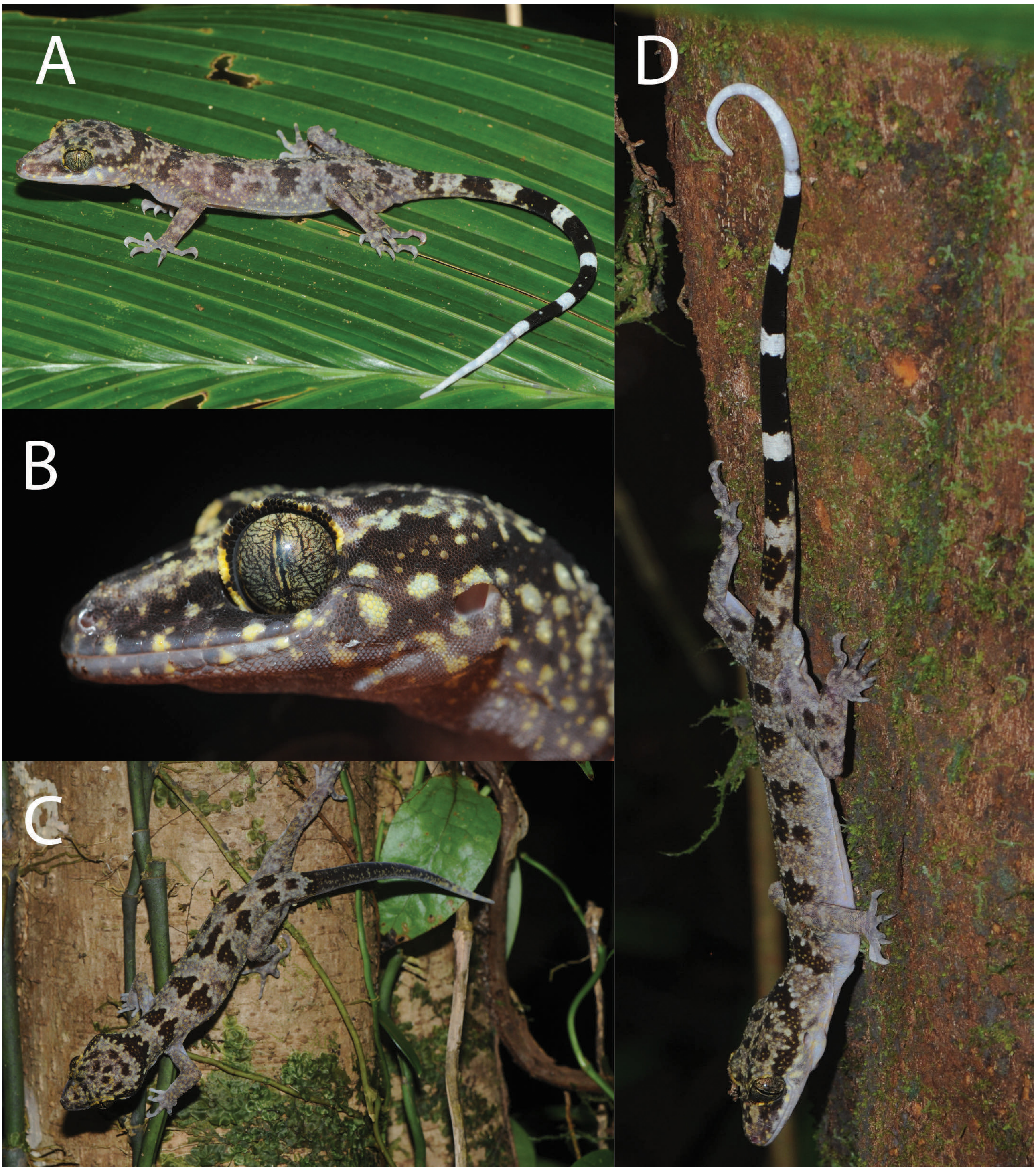

FIGURE 4. *C. crustulus* **sp. nov.** in life, all from type locality near Yeri Village on Manus Island, Papua New Guinea. A) SAMA R71119 (paratype), B) SAMA R71122 (holotype) close up of head, C) uncollected specimen in situ, and D) SAMA R71122 (holotype) in situ. All photographs Stephen Richards.

Body moderately slender (Trk/SVL 0.44), ventrolateral folds distinct and with tubercles that become distinctly larger posteriorly. Dorsum with 17–18 rows of tubercles up to three times width of surrounding small granular scales. Ventral scales much larger than dorsal scales, increasing in size medially, arranged in approximately 49 rows at midpoint of body. No enlarged row of femoral scales. Femoral and precloacal pores absent.

Limbs slender, forelimbs (FA/SVL 0.14) shorter and less robust than hindlimbs (HDL/SVL 0.17). Lateral and dorsal surfaces of upper and lower hindlimbs with numerous low rounded tubercles up to three times size of surrounding granular scales. Digits long and well developed, inflected at basal interphalangeal joints; subdigital lamellae smooth, rounded, undivided and expanded proximal to digital inflection (7–10–10–11–8 manus; 8–13–12–12–7 pes); narrow distal to digital inflection (10–7–7–9–7 manus; 6–10–10–7–4 pes); large recurved claws sheathed by a dorsal and ventral scale.

Tail original, thin and moderately long (123 mm), with obvious dorsal and lateral ridges; scalation irregular, grading from smaller dorsal scales to larger ventral scales; dorsal tubercles extending 21 mm from tail base, and lateral tubercles extending 11 mm from base. Four postcloacal tubercles on each side.

Colouration in preservative. Dorsal and lateral surfaces with beige ground colouration on head, neck, torso and limbs. Body and neck with a series of six dark-brown irregular transverse blotches in pairs (four) or quartets (2) sometimes connected by narrow isthmi, and further indistinct and much lighter brown interstitial blotching or banding. Nuchal band dark brown, continuous with postorbital stripe and with regular scalloping along both anterior and posterior margins. Posterior dorsal region of head with eight irregular dark-brown blotches and further extensive brown maculations, in places tending to form distinctive subcircular markings, especially along the border of the nuchal band. Snout, supra- and interorbital regions, and dorsal edge of supracilaries variegated with light brown to dark brown. Supracilaries dark brown in ventral view, with small number of beige scales. Supralabials ground colour beige, barred with dark brown. Fore- and hindlimbs extensively variegated with light brown to dark brown, with prominent irregular dark-brown blotches on dorsal and posterior edge of hindlimbs, indistinct light-brown barring on fingers and dark-brown barring on toes. Tubercles beige to light-brown across dorsal surfaces, often (but not always) lacking dark-brown pigmentation and contrasting where juxtaposed against dark–brown dorsal blotches. Ventral ground colouration buff across head, torso and forelimbs, darkening around hindlimbs. Palms and fingers with moderately dense-brown maculations; lower hindlimbs, soles and toes with extensive and dense dark-brown maculations. Dorsal and lateral surfaces of tail with seven irregular dark-brown bands of greatly varying width separated by narrower regions of beige with scattered dark-brown flecking. Ventral surface of tail mottled with dark-brown and beige.

Summary measurements of holotype (in mm). SVL 102; TL 123; OT 123; TrK 45.3; HW 19.5; HL 25.9; HH 10.9; OrB 7.8; FA 14.9; HDL 17.8.

Variation. Summary mensural data (in mm) for all adults (four males) in the type series are (mean, with the range in parentheses): SVL 99 (93-102), TrK 45.2 (42.3–45.3), OT (n=2) (116–123); HW 19.2 (17.6–20); HL 25.2 (23.8–26.1); HH 10.9 (10.4–11.2); OrB 7.3 (7.0–7.8);FA 14.6 (14.2–14.9); HDL 17.7 (17.2–18.3). Summary meristic data for these same individuals are: SUPR (to midpoint of eye) 9.2 (9–10); SUPR (rictus of mouth) 11.7 (11–13); INFR 10.5 (10–11); LAMT1 expanded 6.5 (4–8), narrow 7 (7–7); LAMT4 expanded 10.5 (9–12), narrow 11.7 (11–12); DTR 18.4 (18–19); VENT 46.2 (40–49); PCTUB 3–4 on each side.

In colouration all adult paratypes conform broadly with holotype. In pattern, the irregular transverse markings usually consist of pairs or quartets of blotches, but rarely form bands, and may vary slightly in number (SAMA R71121 has five instead of six). The number and configuration of dark-brown blotches on posterior dorsum of head varies (eight on the holotype, seven on SAMA R71120 and SAMA R71121, and six on SJR15092). The venter shows varying density of brown maculations, such that appearance without a microscope varies from cream to light brown, distinct unpigmented ventral ocelli are also present on two paratypes, and tend to be concentrated on throat and lateral surfaces of torso.

The colour pattern and scalation of the single juvenile paratype (SAMA R71119, SVL 75 mm) are similar to that of the adults, consisting of five dark brown transverse markings (three bands and two pairs of blotches). SVL 75, TrK 35.3, OT 83; HW 13.9; HL 19.8; HH 7.8; OrB 5.3; FA 10.9; HDL 13.3. Meristic data for juvenile are: SUPR (to midpoint of eye) 9; SUPR (rictus of mouth) 12; INFR 10; LAMT1 expanded 6, narrow 7; LAMT4 expanded 11, narrow 12; DTR 18; VENT 50; PCTUB 1(L) 3(R) .

Colouration in life. Photographs in life are available for four specimens from the type series (SAMA R71119–22) (Fig. 4). Overall colour is consistent with preserved animals. Numerous small pale-yellow ocelli and spots are present across the dorsal, lateral and ventral surfaces of head, limbs, body and tail, and particularly distinct on supraciliaries, supralabials, posterior of head, and on tubercles across dorsum and lateral fold. Iris pale gold to silvery yellow with extensive dark-brown reticulations.

Comparisons. *C. crustulus* **sp. nov.** does not occur in sympatry with any other species of *Cyrtodactylus*, and it can be readily distinguished from all Melanesian *Cyrtodactylus* apart from *Cyrtodactylus sermowaiensis* by the combination of distinct medial row of transversely enlarged subcaudal scales absent (original tails only); enlarged femoral scales absent; and precloacal or femoral pores absent in males. *C. crustulus* **sp. nov.** further differs from two other *Cyrtodactylus* occurring in the Solomon Islands as follows; from *Cyrtodactylus biordinus* Brown & McCoy by its higher number of dark-brown transverse dorsal markings (5–6 *versus* 2–3), presence of a clear nuchal band (*versus* absent or broken), and postorbital stripe extending to nuchal region only and merging with nuchal band (*versus* extending along torso and not merging with a nuchal band); and from *Cyrtodactylus salomonensis* Rösler, Günther & Richards by its smaller size (adult max SVL 103 mm *versus* 149 mm), lower number of mid-body dorsal tubercle rows (18–19 *versus* 24–29), and in lacking of transversely enlarged subcaudal scales (*versus* present).

Cyrtodactylus crustulus **sp. nov.** is most similar to its close relative *C. sermowaiensis*, with both species lacking a continuous row of transversely enlarged subcaudal scales, enlarged femoral scales and precloacal/femoral pores; however, it differs in aspects of colouration and scalation, specifically: enlarged tubercles across supra- and interorbital regions more numerous (usually >10 *versus* <10); tubercles within dark-brown dorsal bands mostly light brown and contrasting against surrounding dark-brown pigmentation (*versus* tending to be mostly dark-brown and not contrasting against dark-brown colouration of bands); numerous pale-yellow lateral spots on the head and torso in life (*versus* sparse or absent); pale regions on dorsal surfaces of neck and posterior head with indistinct aggregations of light-brown subcircular markings (*versus* at most sparse maculations not forming irregular shapes); and nuchal band with regularly scalloped anterior and posterior edges (*versus* not or irregularly scalloped) (Figs 2, 4).

Etymology. Crustulum "cake". Latin (masculine) meaning cake or pastry; used in reference to the small cake-shaped markings on the posterior dorsal region of the head and similar-shaped indentations along the edges of the nuchal band.

Distribution and Ecology. Known from two localities on Manus Island separated by a distance of approximately 30 kilometres. Specimens at the type locality were observed at night on trees and saplings between one and ten metres off the ground along the banks of a small creek (Fig. 5). Some were observed motionless facing downwards with the head raised in what may be a sit-and-wait hunting posture (Fig. 4D).

FIGURE 5. Streamside lowland rainforest at type locality of *C. crustulus* **sp. nov.** on Manus Island. Five specimens comprising the type series of the new species were collected from small trees and vines at this site. Photograph Stephen Richards.

IUCN status. The two localities known for this species are 30 km apart, suggesting that it is likely to have a broad distribution in rainforest habitats across Manus Island. It appears to be rare and has not been seen in a number of other surveys in apparently suitable habitat. Large areas of Manus are under logging concession or disturbed by small-scale agriculture. Until the distribution, sensitivity and abundance of *Cyrtodactylus crustulus* **sp. nov.** is better understood we suggest listing it as Data Deficient.

Discussion

The genus *Cyrtodactylus* is species-rich and widespread throughout tropical regions of Asia, Wallacea and Melanesia (Wood *et al*. 2012), yet relatively species-poor in the islands east and north of Papua New Guinea; with just two endemic species in the Solomon Islands (Rösler *et al*. 2007; Oliver *et al*. 2017) and one in the Admiralty Islands (this paper). The *Cyrtodactylus sermowaiensis* Group is also one of just two lineages of Melanesian *Cyrtodactylus* found on both mainland New Guinea and distant islands, making investigation of how and when this lineage may have diversified across marine barriers of interest for understanding the biogeographic and geological history of the region.

Tallowin *et al*. (2018) found that the *Cyrtodactylus sermowaiensis* Group was likely to have originated and diversified on terranes that were formerly isolated from the main landmass of New Guinea. In this study, our more detailed sampling of *Cyrtodactylus sermowaiensis* suggests three geographically and potentially genetically distinct populations which broadly overlap with major geological units across northern New Guinea. Specifically, the Adelbert Block within the Finnisterre Terrane, the Torricelli and Prince Alexander Terranes, and the Sepik Terrane along the northern edge of New Guinea's Central Cordillera (Abbott 1995). Of these three blocks, at least the Adelbert block within the Finnistere Terrane may have been separated from the remainder of contemporary New Guinea by a deep-ocean basin until at least the mid-Pleistocene (Abbott 1995). Accordingly, we suggest that apparent structuring within *Cyrtodactylus sermowaiensis* may reflect populations that were historically isolated by sea barriers, that have subsequently been infilled by sediment and uplift. This would lend further support to the hypothesis of an insular history of the Cyrtodactylus sermoiwaiensis Group.

In contrast, *Cyrtodactylus crustulus* **sp. nov.** remains isolated 300 km to the north of contemporary New Guinea in the Admiralty Islands. These islands have never been connected with any other contemporary landmass, hence all terrestrial taxa colonised via overwater dispersal. *Cyrtodactylus crustulus* **sp. nov.** aligns with a suite of taxa on Manus that are nested within clades centred on New Guinea to the south and absent or species depauperate on New Britain, New Ireland, and the Solomon Islands (Zug & Fisher 2012; Timm *et al*. 2016; Tallowin *et al*. 2019). In contrast, some other indigenous taxa in the Admiralty Islands have few or no close relatives in mainland New Guinea and are nested within lineages concentrated in the islands, especially the nearby New Britain and New Ireland (Brown *et al*. 2015; Tonione *et al*. 2015), or even further afield, such as the islands of the former Vitiaz arc (Fiji and Vanuatu) (Austin *et al*. 2010; Oliver *et al*. 2016). *Cyrtodactylus crustulus* **sp. nov.** was inferred to have diverged from other members of the *C. sermowaiensis* Group in the Pliocene (Tallowin *et al*. 2018). This timeframe is comparable with likely age of origin for endemic *Rattus* on Manus (Rowe *et al*. 2008; Timm *et al*. 2016) but younger than other Admiralty Island endemics in radiations that appear to have deeper histories in the island arcs of the southwestern Pacific (Oliver *et al*. 2016). However, while patterns of biogeographic origin and phylogenetic divergence for Manus endemics vary, together they strongly indicate the Admiralty Islands have been continuously emergent and accumulating endemic diversity since the Pliocene, if not earlier. This is consistent with geological studies that also indicate Manus has been subaerial since the late Miocene (Thompson 1952).

The description of *Cyrtodactylus crustulus* **sp. nov.** also serves to further highlight the high endemism and evolutionary significance of the Admiralty islands. In particular, with an area of just over 2000 square kilometres Manus holds six endemic or near-endemic bird species (and numerous further subspecies), four endemic frogs, two endemic mammals, and likely at least five endemic lizards (three of which have been described in the last decade) (Dutson 2011; Whitmore *et al*. 2015). Published and unpublished data suggests at least three additional frog, one bat and several lizard species await description (Whitmore *et al*. 2015; S Richards, P. Oliver unpublished data). Relatively few endemic species in these islands are currently considered threatened. However, some have declined significantly for reasons that are not understood (e.g., the Manus Fantail *Rhipidura semirubra* Sclater) (Whitmore *et al*. 2015), while others seem very rare (e.g., *Lepidodactylus pulcher* Boulenger). Large areas of Manus are also slated for commercial logging operations or affected by subsistence agriculture (Whitmore *et al*. 2015). The vulnerability of evolutionarily similar distinctive insular faunas elsewhere in Australasia to introduced species has been highlighted by recent rapid and unexpected declines on Christmas Island (Oliver *et al*. 2018). Monitoring, effective protection of some areas of primary forest, and ideally development of quarantine protocols, may help to protect against similar declines on Manus.

Acknowledgements

Fieldwork in Papua New Guinea by SJR and CCA was approved by the PNG National Research Institute, and the PNG Department of Environment and Conservation (now the Conservation and Environment Protection Authority). Fieldwork on Manus and Mussau Islands by SJR was facilitated by the Wildlife Conservation Society and permitted by the PNG Department of Environment and Conservation, with support from the Critical Ecosystem Partnership Fund. Surveys on Manus Island were made possible with support and hospitality of the leaders, councillors and residents of Tulu 1 and Piri. Fieldwork in the Sepik River basin was supported by Frieda River Limited and SJR is particularly grateful to Michael Hawikins of FRL for his support. Numerous museum curators and collection managers provided access to specimens and tissues in their care, and in particular we thank Ross Sadlier and Jodi Rowley (Australian Museum), Mark Hutchinson and Carolyn Kovach (South Australian Museum), Andrew Amey and Heather Janetzki (Queensland Museum) and Katie Date, Laura Cook and Diane Bray (Museum Victoria). John Sheridan provided images in Figure 3. We thank Fred Kraus for images and information on *Cyrtodactylus sermowaiensis* and Fred Kraus and Herbert Rösler for constructive reviews. PMO also thanks the Australia Pacific Science Foundation, Queensland Museum and the Environmental Futures Institute at Griffith University for financial support. This work was funded in part by National Science Foundation grant DEB 1146033 to CCA.

References

Abbott, L.D. (1995) Neogene tectonic reconstructions of the Adelbert-Finnisterre-New Britain collision, northern Papua New Guinea. *Journal of South-east Asian Earth Sciences*, 11, 33–51.
https://doi.org/10.1016/0743-9547(94)00032-A

Aplin, K.P., Novera, J. & Armstrong, K.N. (2015) Mammals of Manus and Mussau Islands. *In*: Whitemore, N. (Ed.), *A rapid biodiversity survey of Papua New Guinea's Manus and Massau Islands*. Wildlife Conservation Society, Goroka, pp. 50–68.

Austin, C.C., Rittmeyer, E.N., Richards, S.J. & Zug, G.R. (2010) Phylogeny, historical biogeography and body size evolution in Pacific Island Crocodile Skinks *Tribolonotus* (Squamata; Scincidae). *Molecular Phylogenetics and Evolution*, 57, 227–236.
https://doi.org/10.1016/j.ympev.2010.06.005

Brown, R.M., Siler, C.D., Richards, S.J., Diesmos, A.C. & Cannatella, D.C. (2015) Multilocus phylogeny and a new classification for Southeast Asian and Melanesian forest frogs (family Ceratobatrachidae). *Zoological Journal of the Linnean Society*, 174, 130–196.
https://doi.org/10.1111/zoj.12232

De Rooij, N. (1915) *The Reptiles of the Indo-Australian Archipelago. I. Lacertillia, Chelonia, Emydosauria*. E.J. Brill, Leiden, 384 pp.
https://doi.org/10.5962/bhl.title.5069

Dutson, G. (2011) *Birds of Melanesia*. Christopher Helm, Bedford Square, London, 447 pp.

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1–15.
https://doi.org/10.1093/nar/gkh340

Kraus, F. (2007) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from western Papua New Guinea. *Zootaxa*, 1425 (1), 63–68.
https://doi.org/10.11646/zootaxa.1425.1.8

Kraus, F. (2008) Taxonomic partitioning of *Cyrtodactylus louisadensis* (Lacertilia: Gekkonidae) from Papua New Guinea. *Zootaxa*, 1883 (1), 1–27.
https://doi.org/10.11646/zootaxa.1883.1.1

Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. *Molecular Biology and Evolution*, 33, 1870–1874.
https://doi.org/10.1093/molbev/msw054

Kraus, F. & Allison A. (2006) A new species of *Cyrtodactylus* (Lacertilia: Gekkonidae) from Papua New Guinea. *Zootaxa*, 1425 (1), 59–68.
https://doi.org/10.11646/zootaxa.1425.1.8

Lavery, T.H., Olds, A.D., Seddon, J.M. & Leung, L.K.P. (2016) The mammals of northern Melanesia: speciation, ecology, and

biogeography. *Mammal Review*, 46, 60–76.
https://doi.org/10.1111/mam.12057

Lucky, A. & Sarnat, E.M. (2010) Biogeography and diversification of the Pacific ant genus *Lordomyrma* Emery. *Journal of Biogeography*, 37, 624–634.
https://doi.org/10.1111/j.1365-2699.2009.02242.x

Mayr, E. & Diamond, J. (2001) *The Birds of Northern Melanesia*. Oxford University Press, New York, 548 pp.

Nielson, S.V. & Oliver, P.M. (2017) Morphological and genetic evidence for a new karst specialist lizard from New Guinea (*Cyrtodactylus*: Gekkonidae). *Royal Society Open Science,* 4, 170781.
https://doi.org/10.1098/rsos.170781

Oliver, P.M., Tjaturadi, B., Mumpuni, K.K. & Richards, S. (2008) A new species of large *Cyrtodactylus* (Squamata: Gekkonidae) from Melanesia. *Zootaxa*, 1894 (1), 59–68.
https://doi.org/10.11646/zootaxa.1894.1.5

Oliver, P.M. & Richards, S.J. (2012) A new species of small bent-toed gecko (*Cyrtodactylus*: Gekkonidae) from the Huon Peninsula, Papua New Guinea. *Journal of Herpetology*, 46, 488–493.
https://doi.org/10.1670/11-101

Oliver, P.M., Richards, S.J. & Sistrom, M. (2012) Phylogeny and systematics of Melanesia's most diverse gecko lineage (*Cyrtodactylus*, Gekkonidae, Squamata). *Zoologica Scripta*, 41, 437–454.
https://doi.org/10.1111/j.1463-6409.2012.00545.x

Oliver, P.M., Clegg, J. R., Fisher, R.N., Richards, S.J., Taylor, P. & Jocque, M.M.T. (2016) A new biogeographically disjunct giant gecko (Gehyra: Gekkonidae: Reptilia) from the East Melanesian Islands. *Zootaxa*, 4208 (1), 61–76.
https://doi.org/10.11646/zootaxa.4208.1.3

Oliver, P.M., Travers,S.T., Richmond, J.Q., Pikacha, P. & Risher, R.N. (2017) At the end of the line: independent overwater colonizations of the Solomon Islands by a hyperdiverse trans-Wallacean lizard lineage (*Cyrtodactylus*: Gekkota: Squamata). *Zoological Journal of the Linnean Society*, 182, 681–694.
https://doi.org/10.1093/zoolinnean/zlx047

Oliver, P.M., Brown, R.M., Kraus, F., Rittmeyer, E., Travers, S.L. & Siler, C.D. (2018) Lizards of the lost arcs: mid-Cenozoic diversification, persistence and ecological marginalization in the West Pacific. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20171760.
https://doi.org/10.1098/rspb.2017.1760

Oliver, P.M., Blom, P.P.K., Cogger, H.G., Fisher, R.N., Richmond, J.Q. & Woinarski, J.C.Z. (2018) Insular biogeographic origins and high phylogenetic distinctiveness for a recently depleted lizard fauna from Christmas Island, Australia. *Biology Letters*, 6, 20170696.
https://doi.org/10.1098/rsbl.2017.0696

Oliver, P.M., Karkkainen, D.T., Rösler, H. & Richards, S.J. (2019) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from central New Guinea. *Zootaxa*, 4671 (1), 119–128.
https://doi.org/10.11646/zootaxa.4671.1.9

Radtkey, R.R., Donnellan, S.C., Fisher, R.N., Moritz, C., Hanley, K.A. & Case, T.J. (1995) When species collide: the origin and spread of an asexual species of gecko. *Proceedings of the Royal Society B: Biological Sciences*, 259, 145–152.
https://doi.org/10.1098/rspb.1995.0022

Richards, S.J. & Aplin, K.P. (2015) Herpetofauna of Manus and Mussau Islands. *In*: Whitmore/Nathan, N. *In*: *A rapid biodiversity survey of Papua New Guinea's Manus and Mussau Islands*. Wildlife Conservation Society, Goroka, pp. 31–37

Rowe, K.C., Aplin, K.P., Baverstock, P.R. & Moritz, C. (2008) Recent and Rapid Speciation with Limited Morphological Disparity in the Genus *Rattus*. *Systematic Biology*, 60, 188–203.
https://doi.org/10.1093/sysbio/syq092

Rösler, H., Richards, S.J. & Günther, R. (2007) Remarks on the morphology and taxonomy of geckos of the genus *Cyrtodactylus*, Gray, 1827, occurring east of Wallacea, with descriptions of two new species (Reptilia: Sauria: Gekkonidae). *Salamandra*, 43, 193–230

Sistrom, M.J., Hutchinson, M.N, Hutchinson, R.G. & Donnellan, S.C. (2009) Molecular phylogeny of Australian *Gehyra* (Squamata: Gekkonidae) and taxonomic revision of *Gehyra variegata* in south-eastern Australia. *Zootaxa*, 2277 (1), 14–32.
https://doi.org/10.11646/zootaxa.2277.1.2
https://doi.org/10.5281/zenodo.191131

Stamatakis, A. (2006) RAxML-VI-HPC: Maximum likelihood-based on phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
https://doi.org/10.1093/bioinformatics/btl446

Tallowin, O.J.S., Tamar, K., Meiri, S., Allison, A., Kraus, F., Richards, S.J. & Oliver, P.M. (2018) Early insularity and subsequent mountain uplift were complementary drivers of diversification in a Melanesian lizard radiation (Gekkonidae: *Cyrtodactylus*). *Molecular Phylogenetics and Evolution*, 125, 29–39.
https://doi.org/10.1016/j.ympev.2018.03.020

Tallowin, O.J.S., Meiri, S., Donnellan, S.C., Austin, C.C., Richards, S.J. & Oliver, P.M. (2019) The other side of the Sahulian coin: biogeography and evolution of Melanesian forest dragons. *Biological Journal of the Linnean Society*, 129 (1), 99–113.

https://doi.org/10.1093/biolinnean/blz125

Thompson, J.E. (1952) *Report on the geology of Manus Island, TPNG with reference to the occurrence of bauxite.* Bureau of Mineral Resources, Canberra, 11 pp.

Timm, R.M., Weijola, V., Aplin, K.P., Donnellan, S.C., Flannery, T.F., Thomson, V. & Pine, R.H. (2016) A new species of *Rattus* (Rodentia: Muridae) from Manus Island, Papua New Guinea. *Journal of Mammalogy*, 97, 861–878. https://doi.org/10.1093/jmammal/gyw034

Tonione, M.A., Fisher, R.N., Zhu, C. & Moritz, C. (2015) Deep divergence and structure in the Tropical Oceanic Pacific: a multilocus phylogeography of a widespread gekkonid lizard (Squamata: Gekkonidae: *Gehyra oceanica*). *Journal of Biogeography*, 43, 268–278. https://doi.org/10.1111/jbi.12645

Whitmore, N., Aplin, K., Arihafa, A., Armstrong, K.N., Cuthbert, R., Müller, C.J., Novera, J., Richards, S.J., Tamarua, W., Theischinger, G. & Venter, F. (2015) *A rapid biodiversity survey of Papua New Guinea's Manus and Mussau Islands.* Wildlife Conservation Society Papua New Guinea Program, Goroka, 85 pp.

Wood, P.L., Heinicke, M.P., Jackman, T.R. & Bauer, A.M. (2012) Phylogeny of bent-toed geckos (*Cyrtodactylus*) reveals a west to east pattern of diversification. *Molecular Phylogenetics and Evolution*, 65, 992–1003. https://doi.org/10.1016/j.ympev.2012.08.025

Zug, G.R. & Fisher, R.N. (2012) A preliminary assessment of the *Nactus pelagicus* species group (Squamata: Gekkonidae) in New Guinea and a new species from the Admiralty Islands. *Zootaxa*, 3257 (1), 22–37. https://doi.org/10.11646/zootaxa.3257.1.2

Zug, G.R. (2013) *Reptiles and Amphibians of the Pacific Islands: A Comprehensive Guide*. University of California Press, Berkeley and Los Angeles, California, 306 pp.

APPENDIX 1. Specimen, tissue and Genbank accession numbers for samples from the *Cyrtodactylus sermowaiensis* group included in genetic analyses. Abbreviations for specimens are as follows: ABTC Australian Biological Tissue Collection; AMS Australian Museum Sydney; BPBM Bernice P. Bishop Museum, LSU Louisiana State University; MZB Museum Zoologicum Bogoriense; SJR - Stephen Richards Field number; TNHM Texas Natural History Museum.

Cyrtodactylus crustulus **sp. nov.:** SAMA R71119 SJR15075 ABTC136621 MN640775. SAMA R71121 SJR15076 ABTC136622 MN640776; SAMA R71120 SJR15077 ABTC136623 MN640777; SAMA R71122 SJR15091 ABTC136633 MN640778;

Cyrtodactylus sermowaiensis: ABTC 47761 JQ820296; ABTC50518 AMS R136263 JQ820300; ABTC114694 SJR13191 MN640780; ABTC114956 SAMA R70275 MN640781; ABTC114734 SAMA R70277 MN640783; ABTC114799 SAMA R70276 MN640782; BPBM23317 JX440558; THNM 51540 MN640779.

Cyrtodactylus sp. Karkar: ABTC48695 AMS R124604 MN640774.

APPENDIX 2. Melanesian and Wallacean *Cyrtodactylus* specimens examined. Institutional abbreviations are as follows: American Museum of Natural History (AMNH), Australian Museum (AMS), British Museum of Natural History (BMNH), Museum of Comparative Biology, Harvard (MCZ), Bogor Zoology Museum (MZB), Museum Victoria (NMV), Naturalis, Amsterdam (RMNH), South Australian Museum (SAMA), Western Australian Museum (WAM), and Museum für Naturkunde, Berlin (ZMB).

Cyrtodactylus aaroni Günther & Rösler: ZMB 62275 (holotype), ZMB 62273–4, ZMB 622737, ZMB 62756–7 (paratypes) Indonesia: Papua Barat Province: Wondiwoi Mountains.

Cyrtodactylus arcanus Oliver, Richards & Sistrom: AMS R124599 (holotype), AMS R124599 (paratype) Papua New Guinea: Madang Province: Bundi.

Cyrtodactylus boreoclivus Oliver, Krey, Mumpuni & Richards: AMS R135519 (holotype) Papua New Guinea: Sandaun Province: Torricelli Mountains, Kukumbau area of Mount Sapau; MZB lace 7474–7475, SJR13593–13613 (field numbers, currently at MZB, to be lodged at South Australian Museum) Indonesia: Papua Province: Foja Mountains.

Cyrtodactylus capreoloides Rösler, Richards & Günther: SAMA R62634 (holotype) Papua New Guinea: Southern Highlands Province: Moro; AMS R122412–122414 Papua New Guinea: Southern Highlands Province: Namosado; NMV 75965–75969, Papua New Guinea: Western Province, ~4km east of Kiangabip Village.

Cyrtodactylus darmandvillei (Weber): MZB lace 2005 Indonesia: Komodo National Park: Loh Liang; MZB lace 5297 East Flores: Mount Egon.

Cyrtodactylus derongo Brown & Parker: AMNH 103910 (paratype) Papua New Guinea: Western Province: Derongo Area, Alice River System.

Cyrtodactylus deveti (Brongersma): MZB lace 6036 Indonesia: North Maluku Province: West Halmahera: Weda Village; MZB lace 6037 Indonesia: North Maluku Province: Halmahera: Tosoa Village.

Cyrtodactylus irianjayensis Rösler: MZB lace 5765 Indonesia: Papua Barat Province: Salawati Island.

Cyrtodactylus cf. *irianjayensis*: MZB lace 2297 (seven specimens), 2298 (five specimens) Indonesia: Papua Barat Province: Sorong (from dealers' premises).

Cyrtodactylus loriae (Boulenger): SAMA R62635 Papua New Guinea: Kikori Basin: Darai Plateau; SAMA R62636 Papua New Guinea: Eastern Highlands Province: Crater Mountain Wildlife Management Area: Herowana Village; SAMA R62637 Papua New Guinea: Southern Highlands Province: Moro; SAMA R8305, 8369, WAM R67688–676889 Papua New Guinea: Chimbu Province: Karimui Village.

Cyrtodactylus manos Oliver, Karkkainen, Rösler & Richards: SAMA R62654 (holotype) Papua New Guinea: Southern Highlands Province: Gobe Ridge.

Cyrtodactylus medioclivus Oliver, Richards & Sistrom: SAMA R66091 (holotype) Papua New Guinea: Southern Highlands Province: Wanakipa Village; AMS R122441 (paratype), Papua New Guinea: Southern Highlands Province: Bobole.

Cyrtodactylus mimikanus (Boulenger): BMNH 1946.8.23.5 (syntypes) Indonesia: Papua Province: Mimika River region; MZB lace 3561–3564 Indonesia: Papua Province: Cyclops Mountains: Yongsu; MZB lace 3565–3566 Indonesia: Furu River; MZB lace 2303 (2 specimens) Indonesia: Papua Province: Wapoga River Basin: Siewa.

Cyrtodactylus minor Oliver & Richards: SAMA R65954 (holotype), SAMA R65953 (paratype) Papua New Guinea: Morobe Province: Huon Peninsula: Tarona Camp: 0.5 km South of Yuwong Village: YUS Tree Kangaroo Conservation Project area.

Cyrtodactylus novaeguineae: RMNH 2708A–B (cotypes) Indonesia: Papua Province: Triton Bay area; SAMA R66153–4, SJR10338 (field number, currently at SAMA, to be lodged at PNG National Museum) Papua New Guinea: Western Province: upper Strickland Basin; SAMA R66156 Papua New Guinea: Western Province: Liddel River; AMS R122410 Papua New Guinea: Southern Highlands Province: Waro; SAMA R62648–9 Papua New Guinea: Gulf Province: Libano.

Cyrtodactylus nuaulu Oliver, Edgar, Mumpuni, Iskandar & Lilley: MZB lace 2326 (holotype), MZB lace 2325, 2327–2329 (paratypes) Indonesia: Maluku Province: Seram Island: Manusela National Park.

Cyrtodactylus papuensis (Brongersma): SAMA R62650–2 Papua New Guinea: Gulf Province: Libano; AMS R121227 Papua New Guinea: Western Province: Wipim; AMS R122393–6 Papua New Guinea: Southern Highlands Province: Waro; AMS R122397 Papua New Guinea: Southern Highlands Province: Fogamaiyu.

Cyrtodactylus salomonensis: SAMA R56879 (holotype), SAMA R56780 (paratype) Solomon Islands: Isabel Province: Santa Isabel Island: Kolopakisa.

Cyrtodactylus serratus Kraus: SAMA R62635 Papua New Guinea: Gulf Province: Darai Plateau; SAMA R66155 Papua New Guinea: Western Province: upper Strickland Basin.

Cyrtodactylus sermowaiensis: SAMA R62653 Papua New Guinea: Madang Province: Ramu River Basin; AMS R129288 Papua New Guinea: East Sepik Province: Jama Village; AMS R129289 Papua New Guinea: East Sepik Province: Pukago Village; AMS R130353–6, AMS R136270 Papua New Guinea: West Sepik Province: Wilbeite Village; AMS R135518 Papua New Guinea: West Sepik Province: Imonda Village; AMS R136263 Papua New Guinea: West Sepik Province: 2Fas Village.

Cyrtodactylus tanim Nielsen & Oliver: NMV 75956 (holotype), NMV 75957–75964, SAMA R70319–20 (paratypes) Papua New Guinea: Western Province, all from limestone ranges within 10 km of Kaiangibip Village.

Cyrtodactylus tripartitus Kraus: SAMA R62638–62644 Papua New Guinea: Milne Bay Province: Misima Island.

Cyrtodactylus tuberculatus (Lucas & Frost): SAMA R12058, SAMA 14002 Australia: Queensland: Cooktown.

Cyrtodactylus zugi Oliver, Tjaturadi, Mumpuni, Krey & Richards: MZB lace 5574 (holotype), MZB lace 5573, 5575 (paratypes) Indonesia: Papua Barat Province: south coast of Batanta Island; MZB lace 7310 Indonesia: Papua Barat Province: Batanta.