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Research Article

A new insular species of *Gehyra* (Squamata: Gekkonidae) from Papua New Guinea closely related to *Gehyra oceanica*

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The wide-ranging gecko *Gehyra oceanica* occupies numerous islands across much of the Pacific Ocean basin. Previous work has identified six divergent genetic lineages within lizards assigned to this species. During an expedition to islands off of northern New Guinea we collected lizards of this complex on Crown Island that differ from all other known *Gehyra* in being sexually dimorphic in colour pattern. We find this population to also be genetically divergent to the other lineages previously identified, as we do with another lineage of populations from nearby islands. Given the unique colour pattern of the Crown Island population, combined with its divergent range of precloacal-femoral pores in males and its phylogenetic uniqueness from other members of this complex, we describe this population as a new species, ***Gehyra corona*** sp. nov. currently known only from Crown Island, Papua New Guinea. The discovery of this new species and an additional divergent genetic lineage from within the *G. oceanica* complex highlights the need for further taxonomic revision of that species complex. It seems likely that the new species we identify will prove endemic to Crown Island, but additional islands from around the Bismarck Sea need survey to establish its full range. Given the undisturbed habitat on most of Crown Island and the low human population there, we suggest that this species' IUCN Red List conservation status be Least Concern.

http://zoobank.org/urn:lsid:zoobank.org:pub:299432A3-6AC1-408D-9CCD-ECCB054A78FF

Key words: Bismarck Volcanic Arc, Crown Island, dichromatism, endemism, gecko, sexual dimorphism, species complex

Introduction

Geckos of the genus *Gehyra* comprise 68 species ranging from Thailand and the Ryukyu Islands through Melanesia and Australia, although three species (*G. insulensis*, *G. mutilata*, and *G. oceanica*) mostly range across many of the islands of the Pacific and Indian oceans (Bauer & Henle, 1994; Fisher, 1997; Rocha et al., 2009; Zug, 2013). Fifty species of *Gehyra* are restricted to Australia (Uetz et al., 2023). For the three widespread oceanic species, high genetic uniformity across significant portions of their ranges suggests recent colonizations across much of these vast areas (Rocha et al., 2009) involving both human-mediated (Kraus, 2009) and pre-human (Tonione et al., 2016) dispersals. Most *Gehyra* species are of moderate size (SVL <80 mm), but several species in Melanesia and the Moluccas are much larger (SVL up to 155 mm). Throughout the wide range of this genus, most species are arboreal, but in Australia many species have become saxicolous (Cogger, 2019). Among the islands of the Pacific, *Gehyra* lizards are arboreal and nocturnal, and when multiple species co-occur they are typically of very different body sizes.

Gehyra oceanica is one of the widespread oceanic species, ranging from Palau in the west eastward to the Society, Tuamoto, and Marquesa archipelagos (Bauer & Henle, 1994). It inhabits most of Melanesia, Micronesia, and Polynesia and appears to comprise a species complex. Across this vast distribution, Fisher (1997) discovered using allozyme data that there were two major genetic lineages, one restricted to north of the equator and the other south of the equator, but most of Melanesia was not sampled in that study. He concluded that little to no gene flow occurred between these two populations and noted that this was also consistent with morphological differences between these regions in

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precloacal-femoral pore counts (Beckon, 1992). Beckon's (1992) study was geographically extensive but relied solely on snout-vent length, numbers of precloacal-femoral pores, and numbers of lamellae under the fourth toe. Fisher (1997) hypothesized that the broad ranges attained by each form and the absence of gene flow between them was due to each form dispersing along the oceanic currents in each of those regions, which do not intermix with each other. On the basis of only five specimens, Heinicke et al. (2011) identified four fairly divergent lineages using two nuclear and one mitochondrial gene, but specimen sampling was insufficient to demarcate distributions of those forms across the large geographic range involved. Tonione et al. (2016) extended these analyses by expanded geographic sampling of populations and the use of one mitochondrial and eight nuclear markers. They sequenced mitochondrial cytochrome *c* oxidase subunit 1 (COI) for 173 specimens, estimated relationships among those samples, and then sequenced eight independent nuclear loci for 45 specimens to further test the relationships found using COI. They found consistent evidence of six divergent evolutionary lineages within *G. oceanica* that varied from one another by 7–18% Tamura–Nei divergence in COI and by 0.1–0.6% among the nuclear loci. One of these lineages corresponded to the northern Pacific lineage of Fisher (1997), which they called 'M1'; one to his southern Pacific lineage, which they called 'P1'; and four were endemic to different islands or island groups in northern Melanesia (lineages M2–M5). The widespread northern and southern Pacific lineages were each sister to a different one of the four endemic Melanesian lineages; consequently, northern Melanesia was interpreted as the centre of diversification of this complex. Despite their interpretation that candidate species occur within what is currently called *Gehyra oceanica*, taxonomic follow-up on these studies has been hindered by the relatively minor morphological differences found among these populations (Beckon, 1990, 1992) but especially by the difficulty of comprehensively sampling lizards for morphological features across the vast extent of their distribution. Consequently, formal nomenclatural recognition of the different genotypes has not yet been attempted, nor have more extensive morphological studies been undertaken beyond that done by Beckon (1990, 1992).

In 2018, we (FK, VW) conducted herpetofaunal surveys of four of the small Quaternary volcanic islands of the Bismarck Volcanic Arc west of New Britain. Among our collections was an unusual sample of *Gehyra* '*oceanica*' from Crown Island in which colour pattern seemed to be sexually dichromatic, a rare feature within geckos. In comparing these animals genetically to the samples used in Tonione et al. (2016) we found this sample to represent yet another divergent lineage of Melanesian *G.* '*oceanica*' unsampled in that earlier study. Here we describe these lizards as a new species of *Gehyra* as a first attempt to taxonomically organize species diversity within this complex.

Materials and methods

Molecular methods

We extracted total DNA from liver tissue fixed in 96% ethanol using NucleoSpinTissue kit (Macherey-Nagel) for 17 specimens collected from the Papua New Guinean islands of Crown, Sakar, Tolokiwa, and Umboi. We incubated samples for 2 h following standard protocols for animals or cultured cells.

We amplified the mitochondrial cytochrome *c* oxidase subunit 1 (COI) using the same protocols and primers published previously (Meyer, 2004; Tonione et al., 2011) and used in Tonione et al., 2016. We used this locus to maximize comparison to the geographically extensive findings of Tonione et al. (2016) and because their nuclear loci provided the same patterns shown by COI. Macrogen Europe performed the sequencing. We visualized and assembled chromatograms using Sequencher ver. 5 (Gene Codes Corporation, Ann Arbor, MI). All new sequences are deposited in GenBank (Table 1).

OTU diversity

Our total dataset included 193 OTUs (operational taxonomic units) and 658 characters. In addition to the new sequences produced in this study, our dataset included all *Gehyra oceanica* sequences used in the study by Tonione et al. (2016). We added three other *Gehyra* species (*G. insulensis*, *G. marginata*, and *G. brevipalmata*) as outgroups. We produced multiple sequence alignments applying MAFFT7 online service (Katoh et al., 2019; Kuraku et al., 2013) and inspected the aligned sequences in Mesquite v 3.10 (Maddison & Maddison, 2019).

Phylogenetic analyses

We conducted phylogenetic analyses using the maximum-likelihood method in RAxML v. 8 (Stamatakis, 2014) via the CIPRES portal (Miller et al., 2010). We applied a general time-reversible (GTR) model of sequence evolution (RAxML implements only GTR-based models of nucleotide substitutions) with corrections for a discrete gamma distribution ($GTR + \Gamma$) and estimated branch support values using the rapid

Table 1. Newly sequenced specimens of the *Gehyra oceanica* group used in this study.

Species	Catalogue number	Island	GenBank CO1 acc. no.
Gehyra brevipalmata	USNM 584481	Ngeangas	MH273979
Gehyra insulensis	USNM 564690	Babaldaob	MH273998
Gehyra marginata	NA	NA	AB661662
Gehyra corona sp. nov.	UMMZ 247753	Crown	PP669937
Gehyra corona sp. nov.	UMMZ 247755	Crown	PP669938
Gehyra corona sp. nov.	UMMZ 247756	Crown	PP669939
Gehyra corona sp. nov.	UMMZ 247757	Crown	PP669940
Gehyra corona sp. nov.	UMMZ 247758	Crown	PP669941
Gehyra oceanica M6	UMMZ 247783	Sakar	PP669950
Gehyra oceanica M6	UMMZ 247784	Sakar	PP669951
Gehyra oceanica M6	UMMZ 247785	Sakar	PP669952
Gehyra oceanica M6	UMMZ 247786	Sakar	PP669953
Gehyra oceanica M6	UMMZ 247759	Tolokiwa	PP669942
Gehyra oceanica M6	UMMZ 247760	Tolokiwa	PP669943
Gehyra oceanica M6	UMMZ 247761	Tolokiwa	PP669944
Gehyra oceanica M6	UMMZ 247763	Tolokiwa	PP669945
Gehyra oceanica M6	UMMZ 247522	Umboi	PP669946
Gehyra oceanica M6	UMMZ 247771	Umboi	PP669947
Gehyra oceanica M6	UMMZ 247773	Umboi	PP669948
Gehyra oceanica M6	UMMZ 247774	Umboi	PP669949

bootstrap algorithm with 1000 replicates together with GTR-CAT model (Stamatakis et al., 2008).

We estimated pairwise distances and average evolutionary divergences for COI between and within groups using the Tamura–Nei model (Tamura & Nei, 1993) in MEGA v. 7.0.21 (Kumar et al., 2016; Stecher et al., 2020).

Morphology

We measured snout-vent length of specimens using a ruler, tail length with either a ruler (on straight tails) or a non-elastic string laid along the tail and then placed along a ruler (for curled tails), and all other measurements using either Vernier calipers or a binocular dissecting scope with an attached micrometer. We measured snout-vent length and tail length, and trunk length to the nearest 0.5 mm and all other measurements to the nearest 0.1 mm. Measurements include: snout-vent length (SVL), from tip of snout to vent; trunk length (TrL), from posterior edge of forearm insertion to anterior edge of hindleg insertion; tail length (TL), from vent to tip of tail; tail width (TW), measured at widest point of tail behind the cloacal sacs; head length (HL), directly measured from tip of snout to anterior margin of ear opening, not in lateral projection; head width (HW), maximum width of head; forearm length (FA), from central base of palm to elbow; crus length (CS), from central base of heel to knee; ear diameter (Ear), longest dimension of ear, typically on a diagonal axis; eye diameter (EY), greatest horizontal diameter of eye between the surrounding scales; eye–naris distance (EN), from anteriormost point of eye to centre of naris; snout length (SN), directly measured from anteriormost point of eye to tip of snout, not in lateral projection; internarial distance (IN), distance between centres of nares; ear-to-eye distance (EE), shortest straight-line distance between anterior edge of ear opening to posterior corner of eye; length of the fourth toe, from terminal lamella to the base of the web between T4 and T5 (T4L); width of the fourth toe across its widest point (T4W); length of the series of complete lamellae on the fourth toe (T4lamellaeL); length of webbing between T3 and T4 from base of this webbing to its centre of emargination (T3T4webL), and length of webbing between T4 and T5 from base of this webbing to its centre of emargination (T4T5webL). We counted numbers of supralabials to mid-eye, infralabials to corner of jaw, lamellae (scales at least twice as wide as long) under digits T1 and T4, number of enlarged precloacal-femoral scales in the pore-bearing row, number of precloacal-femoral pores (in males), and number of precloacal scales in a straight line between the apex of the precloacal pore-bearing series and the vent.

We compared specimens of the new species largely with data provided in Beckon (1990), which provided data on SVL, numbers of precloacal-femoral pores in males, and numbers of lamellae under the fourth toe for 340 specimens of *Gehyra oceanica* taken throughout its range. These comprised 160 specimens of lineage P1, 81 specimens of lineage M1, and nine specimens from the Bismarck Islands. These last specimens may comprise a mix of lineages M3 and M5, which are both found on New Britain (Tonione et al., 2016). The

remaining 90 specimens occur more distantly and have no names attached to them yet, so we did not analyse morphological data from them. Beckon (1990) surveyed a wide array of additional characters in *G. oceanica* but focused on these three features as most informative for discrimination within the taxon and did not provide data for the additional characters in his dissertation (Beckon, 1992). We also compared specimens of the new species to museum samples of *G. oceanica* from scattered points in its range (Appendix I) to survey for additional possible features not investigated by Beckon (1990, 1992). Specimens of the new species are deposited in the University of Michigan Museum of Zoology, Ann Arbor, USA (UMMZ); sequences newly generated by us are for those specimens and for two specimens at the United States National Museum, Washington, DC (USNM).

Comparisons

Because what is currently referred to as *Gehyra oceanica* appears to comprise a complex of genetically divergent but morphologically similar species, several of which are geographically restricted in range, we had to decide which populations best reflected true *G. oceanica* for comparison to our new species. We further had to determine which, if any, names currently in synonymy might apply to other of the identified genetically divergent lineages that may be viewed as currently unrecognized species. The original description of *G. oceanica* (Lesson, 1831) was imprecise as to identifying a single type locality, so Wermuth (1965) restricted it to Tahiti and Borabora in the Society Islands. Hence, the name would seem most likely to apply to the southern Pacific lineage (P1) identified by Fisher (1997) and Tonione et al. (2016), although the Micronesian lineage (M1) also occurs in that region at lesser frequency, perhaps having been recently introduced. It has been asserted that the existing types are from Tongatapu and Kosrae (Bauer & Henle, 1994) and not the Society Islands. However, the original illustration of *G. oceanica* (Lesson, 1830) serves as the holotype for that species (Lescure, 2015), and it remains uncertain whether it matches any of the specimens in the Paris Museum that have been referred to as types (G. Shea, pers. comm.). Furthermore, the specimen illustrated was collected during the *La Coquille* Expedition, which did not visit Tongatapu or Kosrae, providing another reason why those MNHN specimens cannot be types (G. Shea, pers. comm.). As well, *Hemidactylus oualensis* Duméril and Bibron is currently in the synonymy of *G. oceanica*. It was originally described from Oualen [Kosrae], Tahiti, Vanikoro, and Tongatapu, but Wells and Wellington (1985) designated MNHN 1776 from Kosrae in the Federated States of Micronesia as the lectotype of this species, leaving that name to presumably apply to the Micronesian lineage (M1) of *G. oceanica*, although this remains unverified at present because neither Fisher (1997) nor Tonione et al. (2016) sampled *G. oceanica* specifically from that island. The identity and taxonomy of *Gehyra pacifica* Gray – also currently placed in the synonym of *G. oceanica* – is even more confused than these names, and it is currently the topic of study by G. Shea. Its type locality of 'Insulâ quadam Oceani Pacifici' ['a certain island in the Pacific Ocean'] places it in one of the widespread (P1 or M1) lineages of *G. oceanica* discussed above.

Given this nomenclatural information, it is clear that diagnosis of any distinct Pacific taxa closely related to *Gehyra oceanica* must involve comparison against both the P1 (likely true *G. oceanica*) and M1 (likely *G. oualensis*) lineages identified by Fisher (1997) and Tonione et al. (2016) to ensure that the new taxon does not inadvertently become a synonym of one of these already-named lineages. Hence, we compare our new species to both these lineages as well as to geographically proximate samples from other Bismarck islands. We compare our Crown Island sample molecularly to all the *G. oceanica* samples used by Tonione et al. (2016).

Results

We identified eight genetic clades within the *Gehyra oceanica* group that received very strong support (bootstrap values of 97–100%) in our maximum-likelihood analysis (Fig. 1). These clades include the six (*G. oceanica* lineages M1–M5, P1) previously identified by Tonione et al. (2016) as well as our samples from Crown Island (described below) and from adjacent Sakar, Tolokiwa, and Umboi islands (which we herein designate as 'M6', following the schema of Tonione et al., 2016). The population from Crown Island clustered with *G. oceanica* lineages P1 and M5 in an essentially unresolved trichotomy, whereas geographically adjacent lineage M6 was distantly related to the Crown Island lineage (Fig. 1, Table 2) and clustered with lineage M4 from the central Solomon Islands. Aside from this trichotomy, support values for internal branches in the tree were generally fairly high (86–99%) though not as robust as values identifying each lineage (Fig. 1). Divergence values for COI among these eight lineages were high (Table 2) and averaged 24–61 times the intra-lineage divergences seen in the Crown Island lineage and 24–48 times the intra-lineage divergences seen in

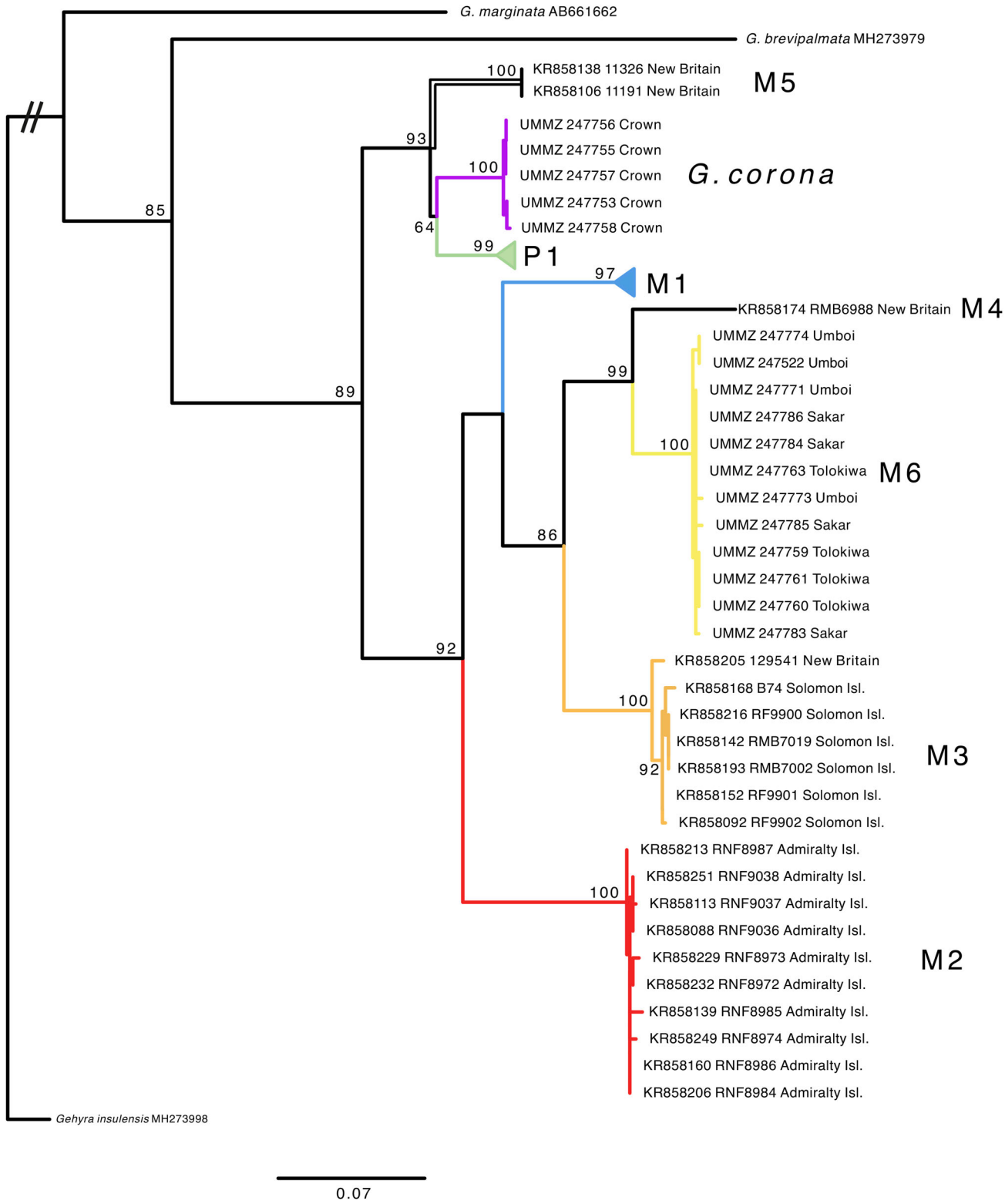

Fig. 1. Maximum-likelihood tree of *Gehyra oceanica* group, with bootstrap values >80% shown for each internal branch. Tree rooted with *Gehyra insulensis* as outgroup. Scale bar corresponds to mean number of nucleotide substitutions/site.

Table 2. Mean genetic distances among lineages of the *Gehyra oceanica* complex and the outgroups used in this study.

	***Gehyra brevipalmata* (*n* = 1)**	***Gehyra insulensis* (*n* = 1)**	***Gehyra marginata* (*n* = 1)**	***Gehyra corona* sp. nov. (*n* = 6)**	**M1 (*n* = 31)**	**M2 (*n* = 10)**	**M3 (*n* = 7)**	**M4 (*n* = 1)**	**M5 (*n* = 2)**	**M6 (*n* = 12)**
G. insulensis	0.3005									
G. marginata	0.2258	0.2641								
G. corona sp. nov.	0.2213	0.2793	0.2260							
M1	0.2198	0.2765	0.2158	0.1496						
M2	0.2190	0.2728	0.2269	0.1285	0.1218					
M3	0.2230	0.2954	0.1971	0.1433	0.1253	0.1421				
M4	0.2263	0.3017	0.2120	0.1707	0.1247	0.1333	0.1102			
M5	0.2258	0.2574	0.2335	0.0722	0.1537	0.1564	0.1609	0.1804		
M6	0.2160	0.2856	0.1959	0.1512	0.1230	0.1260	0.0964	0.0786	0.1540	
P1 (*n* = 122)	0.2150	0.2704	0.2146	0.0669	0.1367	0.1506	0.1532	0.1616	0.0662	0.1486

Values calculated using the Tamura-Nei (Tamura & Nei, 1993) model. Individuals within each group are shown in Fig. 1 except the large number of individuals in groups P1 and M1 are listed in Tonione et al. (2016).

Table 3. Genetic variation in COI thin lineages of the *Gehyra oceanica* complex.

		Divergence	
Lineage	***N***	**Mean**	**Range**
Gehyra corona sp. nov.	5	0.0028	0–0.0053
Gehyra oceanica M1	31	0.0060	0–0.0139
Gehyra oceanica M2	10	0.0036	0–0.0080
Gehyra oceanica M3	7	0.0051	0–0.017
Gehyra oceanica M4	1	—	—
Gehyra oceanica M5	2	0	0
Gehyra oceanica M6	12	0.0032	0–0.0089
Gehyra oceanica P1	122	0.0007	0–0.0053

Values calculated using the Tamura-Nei (Tamura & Nei, 1993) model.

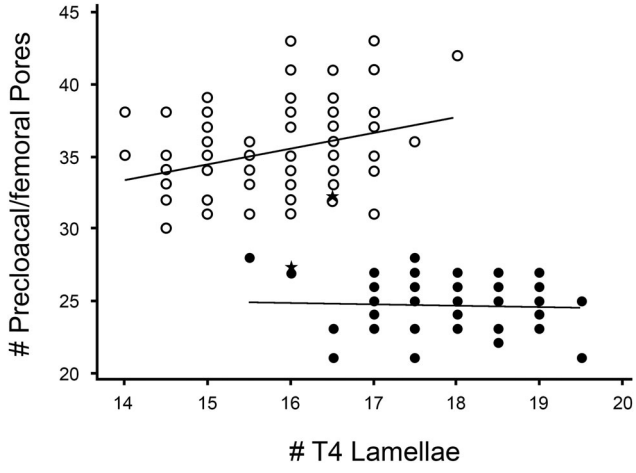

Fig. 2. Scatterplot of numbers of precloacal-femoral pores against numbers of T4 lamellae for the male samples of Crown Island (stars), Polynesian (open circles), and Micronesian (closed circles) *Gehyra oceanica*. Regression line for the Polynesian sample is $y = 1.09x + 18.1$, $R^2 = 0.099$; regression line for the Micronesian sample is $y = -0.08x + 26.1$, $R^2 = 0.002$.

the M6 populations (Table 3). Inter-lineage divergence values for the six lineages previously identified by Tonione et al. (2016) were even higher (Table 2), with most intra-lineage divergences ranging approximately the same as those seen in the Crown Island and M6 lineages, though lineage P1 was especially uniform (Table 3).

Contrasts of numbers of precloacal-femoral pores in males against numbers of T4 lamellae make clear that the Polynesian and Micronesian lineages of *G. oceanica* are readily distinguished from each other; however, little of the variance within each cloud is explained by regression of the two variables, with $y = 1.09x + 18.1$, $R^2 = 0.099$ for the Polynesian sample, and $y = -0.08x + 26.1$, $R^2 = 0.002$ for the Micronesian sample, indicating the developmental independence of the two features and supporting their use as independent diagnostic features. The two available Crown Island samples fall between the Polynesian and Micronesian clusters and slightly overlap each (Fig. 2), suggesting that they are likely to form a third, intermediate cloud that may be further tested once additional samples become available.

Gehyra corona sp. nov.

Figs 3A, B, 4

Holotype. UMMZ 247756 (field tag FK 17752), mature male, collected by F. Kraus and V. Weijola on Crown Island, 5.1231°S, 146.9760°E, ~30 m a.s.l., Madang Province, Papua New Guinea, 12 March 2018.

Paratypes (n = 5). UMMZ 247757–58, same data as holotype; UMMZ 247753–55, same data as holotype except collected 11 March 2018.

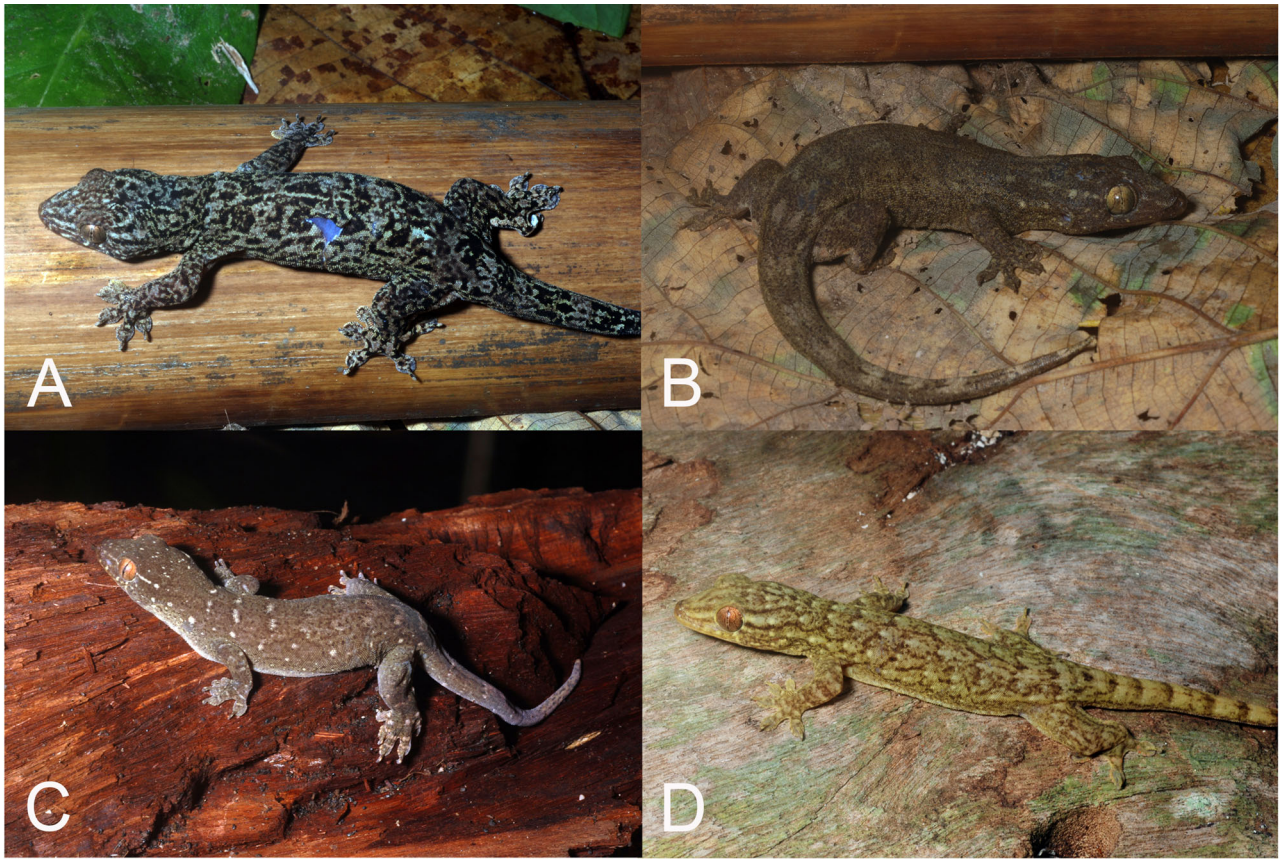

Fig. 3. Portraits in life of members of *Gehyra corona* and *G. oceanica* lineage M6 from nearby islands of the Bismarck Volcanic arc. (A) male *G. corona* paratype from Crown Island (UMMZ 247754), (B) female *G. corona* paratype from Crown Island (UMMZ 247755), (C) *G. oceanica* lineage M6 from Tolokiwa Island (UMMZ 247759), and (D) *G. oceanica* lineage M6 from Umboi Island (UMMZ 247771). In none of the islands near to Crown Island did we find morphotypes similar to male *G. corona.*

Diagnosis. An intermediately sized (adult female SVL 75–88 mm, adult male 79–95 mm) species of *Gehyra* having entirely undivided subterminal lamellae on all toes; 16–19 T4 lamellae; 12–15 T1 lamellae; extensive webbing between all toes; 27–32 precloacal-femoral pores in a continuous row in males; small and subequal subcaudal scales; rounded tail lacking serrations; lateral, antecubital, and popliteal skin folds absent or weakly developed; and colour pattern sexually dimorphic, with males boldly maculated with dark brown dorsally (Fig. 3A) and females grey irregularly suffused with brown and with whitish or pale-grey dots on neck and head (Fig. 3B).

This species is easily distinguished from most other *Gehyra* by having both undivided subapical lamellae under the toes and small, subequal subcaudal scales. Only *G. marginata* and *G. oceanica* also have those features. *Gehyra corona* may be distinguished from *G. marginata* by its smaller size (SVL = 75–95 mm vs. 130–142 in *G. marginata*), rounded (vs. flattened) tail, fewer T4 lamellae (16–19 vs. 20–27 in *G. marginata*), and lack of lateral, antecubital, and popliteal skin folds (vs. skin folds prominent in *G. marginata*).

Gehyra corona is most similar to *G. oceanica* and was included under that species by Beckon (1990). It may be distinguished from the widespread Polynesian lineage (P1) of *G. oceanica* by averaging fewer femoral-precloacal pores in males (mean = 29.5, range = 27–32, $n = 2$ vs. mean = 35.3, range = 30–43, $n = 81$ in Polynesian lineage PI) and a higher average number of T4 lamellae (mean = 17.4, range = 16–19, $n = 12$ digits vs. mean = 15.7, range = 13–19, $n = 314$ digits in Polynesian lineage PI). It differs from the widespread Micronesian lineage (M1) by having, on average, more precloacal-femoral pores in males (mean = 29.5, range = 27–32, $n = 2$ vs. mean = 24.2, range = 21–28, $n = 56$ in Micronesian lineage M1). Differences among these lineages for these two features are most readily seen graphically (Fig. 2).

As well, *Gehyra corona* differs from the geographically adjacent sample of *G. oceanica* from the Bismarck Islands in having, on average, fewer precloacal-femoral pores in males (mean = 29.5, range = 27–32, $n = 2$ vs. mean = 36.0, range = 31–42, $n = 5$ in Bismarck *G. oceanica*) and slightly more T4 lamellae (mean = 17.4, range = 16–19, $n = 12$ digits vs. mean = 16.2, range = 15–19, $n = 18$ digits in Bismarck *G. oceanica*). *Gehyra corona* is distinguished from all those lineages and all other *G. oceanica* reported in the literature in being (presumably sexually) dimorphic in colour pattern, with our two males boldly blotched and mottled with dark brown dorsally (Fig. 3A) and our four females brown or grey irregularly suffused with vague darker-brown saddles and with whitish or pale-grey dots on neck, head, and sometimes on hindlimbs (Fig. 3B). These contrast with the spotted patterns seen in nearby *G. oceanica* lineage M6 (Fig. 3C, D) and with the uniformly grey to vaguely spotted patterns seen in other lineages of *G. oceanica*.

Description of holotype. A mature male of fairly large size (SVL = 95.0 mm) with a right-lateral incision behind the pectoral region; liver removed. Head relatively long (HL/SVL = 0.26) and wide (HW/HL = 0.81), distinct from neck (Fig. 4A). Loreal region slightly inflated; no distinct canthus rostralis. Top of snout, area between nares, and area above central supralabials shallowly concave. Snout tapered and rounded at tip, relatively long (SN/HL = 0.44), more than twice eye diameter (SN/EY = 2.2). Eye of modest size (EY/HL = 0.20, EY/EN = 0.58); pupil vertical, constricted into series of four lobes; anterior supraciliaries slightly larger than adjacent granules, posterior ones subequal to adjacent granules. Ear opening small (Ear/HL = 0.082), narrowly compressed, oriented obliquely; distance between ear and eye considerably larger than eye diameter (EE/EY = 1.8). Rostral one-and-two-thirds as wide (4.0 mm) as high (2.4 mm), highest just medial to nares, lower between these points; length 0.90 mm. Supranasals separated by single internasal along posterior rostral margin. Rostral in contact with first supralabials, two supranasals, and one internasal. External nares circular; each bordered by rostral, single supranasal, first supralabial, and three postnasals. Mental triangular, 3.8 mm wide. Mental bordered posteriorly by two elongate postmentals, these bordered posteriorly by tiny granular scales subequal to those on chin (Fig. 4B). Postmentals bordered laterally by similarly elongate subinfralabials, gradually decreasing in size laterally; a small scale between second and third of these scales on each side. First three infralabials bordered below by single subinfralabial; next three infralabials bordered below by two rows of smaller subinfralabials that are still much larger than adjacent chin granules. Supralabials to mid-orbital position 10 (R) or 11 (L); three small supralabials posterior to this; angle of jaw bordered with granular scales. Infralabials 13 on each side.

Body of fairly robust habitus (TrL/SVL = 0.45), slightly depressed. Dorsal scales on head, body, limbs, and throat small juxtaposed granules, smaller on neck, head, and limbs, largest on sides and dorsum; tubercles absent. Ventral scales larger, flat, smooth, subimbricate, larger posteriorly than anteriorly, gradually decreasing in size laterally to become granular. Small lateral fold present on body; popliteal and antecubital folds absent.

Enlarged precloacal-femoral scales in single series of 35 scales extending in a curved chevron to centre of each thigh (Fig. 4C), 32 of these containing pores; thigh scales anterior to this row flat, subimbricate, larger than those posterior to row, which are round and subimbricate to granular. Enlarged, imbricate scales form a pubic patch between precloacal series and vent, decreasing in size posteriorly; 10 scales in a row between apex of enlarged precloacal series and vent. Scales under arms granular, those under hindlimbs enlarged, flat, imbricate; scales on palms and soles rounded, flattened, smooth, subimbricate.

Fore- and hindlimbs well-developed (FA/SVL = 0.11, CS/SVL = 0.14). Digits well-developed, with broad pads on toes (T4W/T4L = 0.56), all but first fingers and toes with recurved claws; clawed terminal phalanges laterally compressed, free above, arising from toe pad, inset from its margin, extending slightly beyond it. Subdigital lamellae narrow and smooth, all undivided, most forming a shallowly curved chevron medially (Fig. 4D); lamellae extend for more than half length of each toe (T4lamellaeL/T4L = 0.65). Lamellae of manus 14–17–17–16–15 on right, 14–16–17–16–16 on left; of pes 14–17–18–17–16 on right, 14–17–15–16–16 on left. Relative lengths of digits on manus and pes I < II < III ≈ V < IV. Webbing present between all digits, most extensive between T3 and T4 (T3T4webL/T4L = 0.20, T4T5webL/T4L = 0.18).

Tail seemingly complete, with enlarged granular scales dorsally, becoming flat and imbricate posteriorly; under tail with several rows of enlarged, flat, imbricate scales, larger mid-ventrally. Cloacal sacs swollen, with single small external orifice situated near each lateral margin of vent; three slightly enlarged, blunt postcloacal spurs on each side of tailbase; midventral scales of sac flat, subimbricate, larger posteriorly, slightly larger than those ventrolaterally.

Colour in preservative. Dorsal ground colour on body, head, and limbs grey, irregularly marked with dark-brown vermiculations and ragged spots, denser on head, limbs, tail, and sides than centre of trunk. Venter dirty

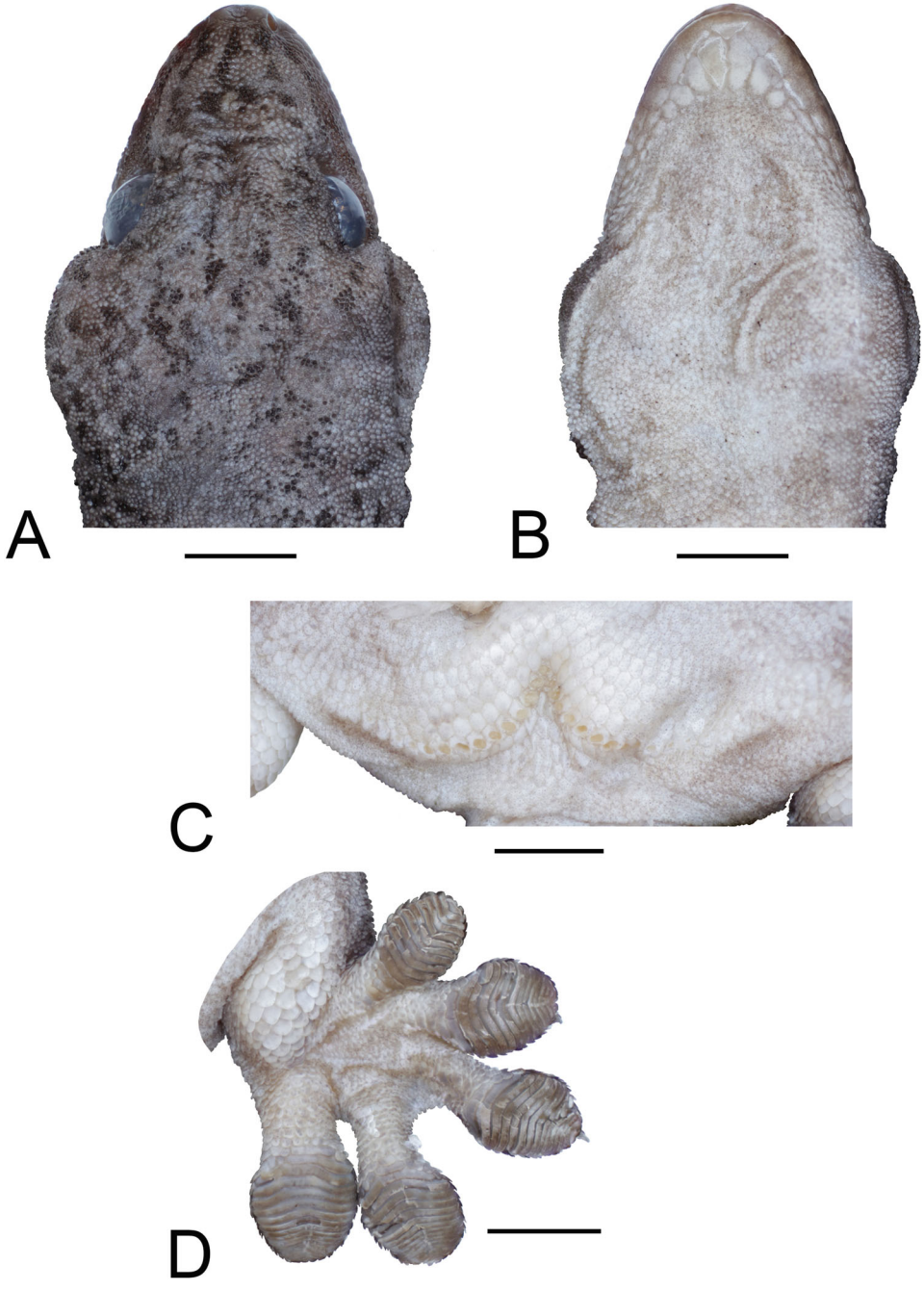

Fig. 4. Holotype of *Gehyra corona*, UMMZ 247756. (A) dorsal view of head, (B) ventral view of head, (C) pubic region showing precloacal pore series, and (D) left foot. Scale bars = 5 mm.

white, paler around precloacal area; lamellae darker grey than palms and soles. Iris tan heavily vermiculated with dark brown.

Measurements (in mm). SVL = 95.0, TrL = 42.5, FA = 10.9, CS = 13.0, HL = 24.3, HW = 19.6, HH = 12.2, Ear = 2.0, EE = 8.8, EY = 4.9, SN = 10.8, EN = 8.5, IN = 3.6, T4L = 8.0, T4W = 4.5, T4lamellaeL = 5.2, T3T4webL = 1.6, T4T5webL = 1.4.

Variation. Greatest mensural variation of importance in the sample of *Gehyra corona* are in features of the toes (Table 4), which in part likely reflects difficulty of measuring these structures if the toes are not preserved in a perfectly flat and spread position. Meristically,

Table 4. Mensural and meristic data for the type series of *Gehyra corona* sp. nov.

Character	UMMZ 247753 paratype	UMMZ 247754 paratype	UMMZ 247755 paratype	UMMZ 247756 holotype	UMMZ 247757 paratype	UMMZ 247758 paratype
Sex	F	M	F	M	F	F
SV	84.0	79.0	75.0	95.0	88.0	83.5
TrunkL/SV	0.49	0.43	0.45	0.45	0.47	0.44
CrusL/SV	0.14	0.14	0.14	0.14	0.14	0.14
TailL/SV		0.76	0.87	0.91		0.93
TailW/SV	0.09	0.11	0.11	0.12	0.10	0.10
HL/SV	0.25	0.26	0.26	0.26	0.24	0.23
HW/SV	0.19	0.20	0.19	0.21	0.18	0.19
ForearmL/SV	0.11	0.13	0.13	0.11	0.12	0.11
HW/HL	0.76	0.76	0.73	0.81	0.74	0.82
EarL/HL	0.079	0.096	0.092	0.082	0.061	0.078
SN/HL	0.42	0.43	0.45	0.44	0.45	0.45
EY/HL	0.22	0.20	0.22	0.20	0.23	0.23
SN/EY	1.9	2.1	2.1	2.2	1.9	2.0
EY/EN	0.64	0.58	0.61	0.58	0.65	0.62
EE/EY	1.36	1.67	1.37	1.76	1.38	1.50
T4L/SV	0.090	0.089	0.087	0.093	0.091	0.096
T4W/T4L	0.43	0.49	0.46	0.51	0.49	0.46
T4 scansor L/T4L	0.55	0.66	0.63	0.60	0.59	0.61
T3-T4 web L/T4L	0.20	0.20	0.18	0.18	0.18	0.19
T4-T5 web L/T4L	0.11	0.11	0.15	0.11	0.15	0.10
#T4 scansors	17\17	16\16	18\18	17\16	17\17	18\18
#T1 scansors	15\15	12\13	14\14	13\14	14\14	14\13
# Supralabials to mid-eye	10\10	10\9	11\11	10\11	11\11	11\10
# Infralabials	13\12	13\12	14\13	13\13	14\13	14\13
# Enlarged precloacal-femoral scales	25	33	31	35	27	30
# Precloacal-femoral pores	0	27	0	32	0	0

variation in numbers of lamellae under the first and fourth toes are similar to that seen in other populations of the *G. oceanica* complex. Numbers of enlarged precloacal-femoral scales is more variable due to the sometimes gradual decrease in size of these scales laterally and the difficulty of identifying the lateral terminus of these scales in females, which lack pores to more easily guide the counting.

Colour pattern is the character showing greatest variation in this species. Males are boldly maculated with dark brown spots, flecks, and vermiculations on a pale or medium-grey background (Fig. 3A). In contrast, females are mostly uniform pale brown dorsally (Fig. 3B), although UMMZ 24755 also has several slightly darker-brown flecks scattered over the dorsum. In preservative, venters of all specimens are dirty white.

Colour in life. Field notes for UMMZ 247753, a female, read 'Dorsum milk-chocolate brown with vague darker-brown crossbands. Vaguely defined yellow-gray spots on back of head and neck, above rear-leg insertion, and on rear legs. Venter uniform deep lemon yellow. Lamellae pale gray. Iris milk-chocolate brown.' Male UMMZ 247754 was pale brown highly maculated with dark brown (Fig. 3A); its venter was pale lemon yellow. Female UMMZ 247755 had more of a greyish-brown ground colour than UMMZ 247753 (Fig. 3B), and UMMZ 247757 was similar to UMMZ 247753 but with the venter brown with a little yellow wash, especially posteriorly.

Etymology. The species name is the Latin noun for 'crown', named for the sole island from which this species is named.

Range. Known only from a single locality on the eastern end of Crown Island (Fig. 5). The species very likely ranges across the coastal and low-forested areas of Crown Island. Crown Island is a steep, extinct,

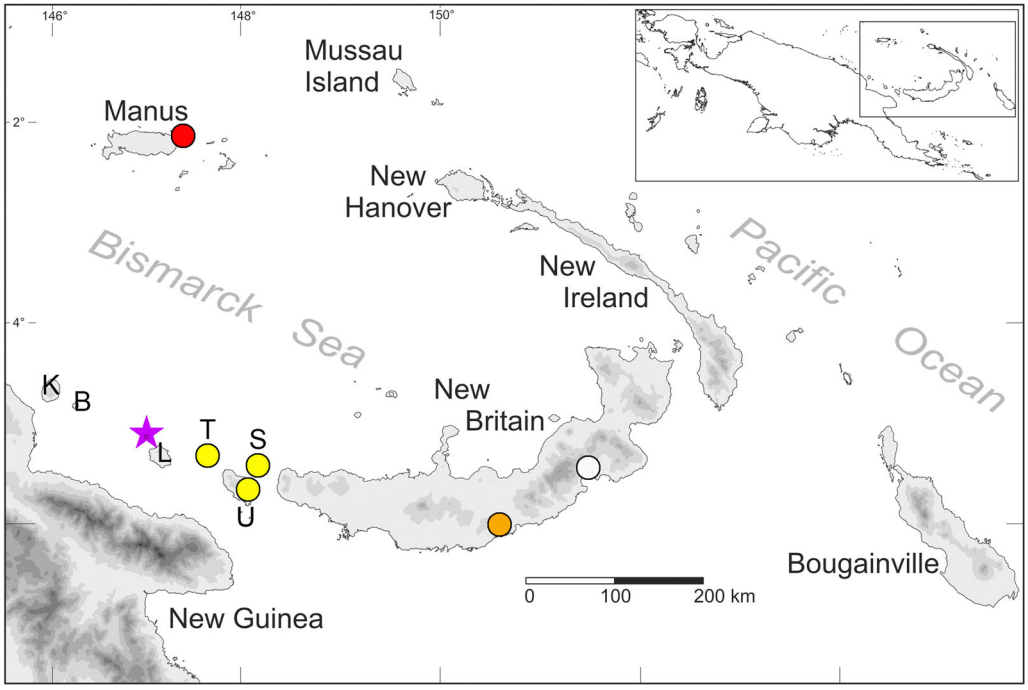

Fig. 5. Map of the Bismarck and Admiralty islands showing the type locality of *Gehyra corona* on Crown Island (purple star); nearby populations of *G. oceanica* lineage M6 (yellow circles) on Sakar Island (S), Tolokiwa Island (T), and Umboi Island (U); *G. oceanica* lineages M3 (orange circle) on central New Britain and M5 (white circle) on eastern New Britain; and lineage M2 (red circle) from Manus Island. Population colours match those in Fig. 1. Other islands referred to in the text: B: Bagabag Island; K: Karkar Island; L: Long Island.

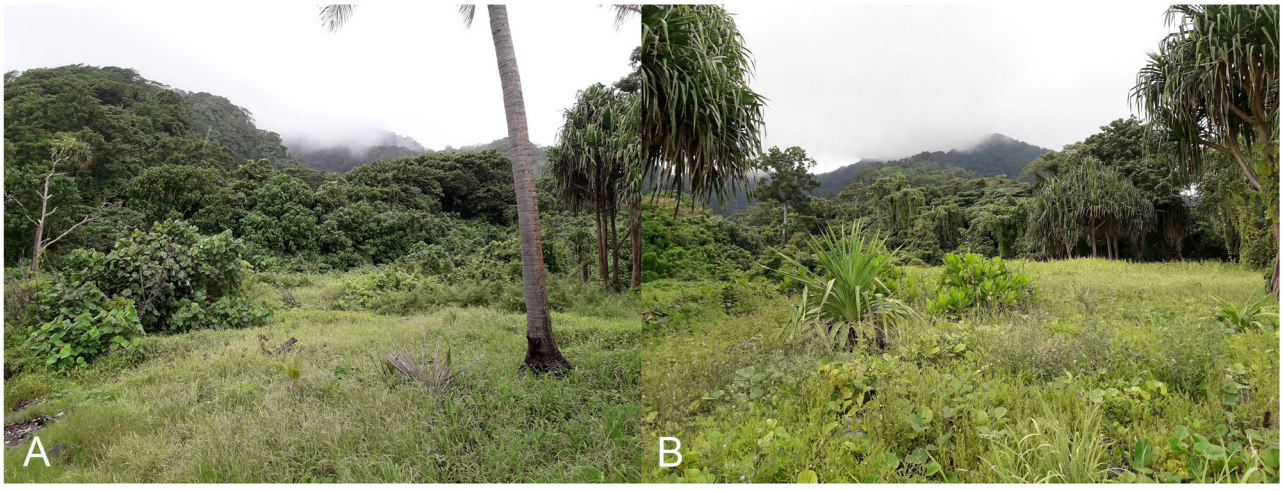

Fig. 6. Habitat around the type locality of *Gehyra corona* on Crown Island from which lizards were collected on tree trunks.

Quaternary volcanic cinder cone of 14.75 km^2 and 566 m elevation (Johnson et al., 1972). If we are correct in our estimate that this species inhabits only low-elevation habitats near the coast (based on the habits of other members of the *Gehyra oceanica* complex), its total area of occupancy will be <1000 ha and possibly considerably less than this.

Ecology. The type series was collected active at night in disturbed low-elevation forest near (but not on) the coast (Fig. 6). All animals came from tree trunks, including on *Pandanus* (presumably *P. tectorius*) and *Cocos nucifera*.

The smaller male (SVL = 79 mm) has weakly developed pores and small testes, suggesting that it is just

attaining sexual maturity; the holotype (SVL = 95 mm) is a mature male. The two largest females (SVL = 84 and 88 mm) have mature eggs in the abdominal cavity.

Remarks. The colour-pattern dimorphism seen in our specimens appears to be sexually dimorphic; however, the sample size is small, and a binomial test for sexual segregation of colour pattern attains only $p = 0.23$, not allowing us to be certain that pattern does not sort randomly across the sexes. Hence, although dramatic pattern dimorphism in this species is real and discontinuous, whether it is truly sexually dimorphic requires a larger sample size to establish.

In any event, the colour-pattern dimorphism and the range of subdigital lamellar counts clearly preclude assignment of these lizards to either lineages P1 or M1 of *G. oceanica*, to which the names *G. oceanica* and *G. oualensis* are likely to apply once the nomenclatural history and taxonomic relationships among them become clearer.

Discussion

Gehyra oceanica has typically been identified as those members of the genus of moderate size, with extensive webbing between the toes, fewer than 20 undivided T4 lamellae, unenlarged subcaudals, and no lateral serrations on the tail. Studies of the past few decades have shown, however, that there has been unrecognized morphological (Beckon, 1992) and molecular (Fisher, 1997; Heinicke et al., 2011; Tonione et al., 2016) variation across this wide-ranging species that suggests that *G. oceanica* forms a species complex. However, diagnosis of the lineages involved has not advanced very far because of the difficulty of sampling extensively across the broad range of this species, the paucity of morphological features that distinguish the few lineages examined, and inadequate samples for some of the identified lineages. This study takes an initial step toward formally recognizing species diversity within this complex by describing *G. corona* based on its unique colour-pattern dimorphism and diagnostic range of precloacal-femoral pores while recognizing its divergent genetic signature. This species cannot be credibly assigned to *G. oceanica* or its current synonyms based on either morphology or genetics. The relative paucity of morphological differentiation among the lineages of *G. oceanica* is similar to that seen between other recently recognized species within *Gehyra* (Fisher, 1997; Heinicke et al., 2011; Rocha et al., 2009) and *Bavayia* Roux (Bauer et al., 2022). In those instances, species were first postulated based on high molecular divergences or phylogenetic results that suggested evolutionary independence of lineages, and then followed (in the case of *Bavayia*) with morphological diagnoses based on slight differences in colour pattern or size. In the case of *G. corona*, we first recognized this species as morphologically distinctive in the field and then confirmed its evolutionary independence with molecular and additional morphological data, as presented herein. Nonetheless, morphological diagnosis against *G. oceanica* is still relatively subtle compared with that seen in many other Melanesian lizards.

Our study expands on the growing knowledge of genetic lineages within the *Gehyra oceanica* complex by identifying two additional divergent molecular lineages within Melanesia, the region previously found to contain the greatest genetic diversity within this complex (Tonione et al., 2016). We describe the first lineage as *G. corona*, and we note that the second lineage (M6) appears most closely related to lineage M4, known only from a single specimen from Ranongga Island, 1150 km southeast of our samples. It is of interest that the lowest genetic divergence value discovered between the lineages identified by Tonione et al. (2016) was 7%, between lineages P1, which is widespread across the southern Pacific, and M5, which is currently known only from eastern New Britain (Fig. 5). The closest geographic approach of these lineages, as currently known, is 1760 km. The new lineages we herein identify (*G. corona*, M6) approximate this same degree of genetic divergence, with *G. corona* being 6.7% divergent from lineage P1 and 7.5% divergent from the geographically nearer lineage M5, whereas lineage M6 is 7.9% divergent from the remote lineage M4. The fact that *G. corona* is morphologically distinctive and readily diagnosed from other populations of *G. oceanica* even at these lower levels of genetic divergence supports the supposition that each of the genetic lineages identified by Tonione et al. (2016) and by us represents a currently undescribed species. This is also suggested by the fact that the geographically nearest population of *G.* '*oceanica*' (lineage M6, 60 km distant on Tolokiwa Island) is 15% genetically divergent to *G. corona* instead of shallowly divergent. Alternatively, it is often the case that mitochondrial DNA divergences do not correlate with species boundaries (e.g., Ballard et al., 2002; Ferris et al., 1983; Gaultier et al., 2009), so it may be argued that these lineages do not represent independent species but merely random genetic variation within a single wide-ranging *G. oceanica*. Against this supposition are the high degree of genetic divergences among these populations (Table 2), the geographic sorting of these lineages, Bayesian posterior probabilities that supported the evolutionary independence of the lineages identified by Tonione et al. (2016) as candidate

species, and our results showing *G. corona* to be morphologically unique and falling out among some of these other divergent lineages. Consequently, we think it likely that the six genetic lineages identified by Tonione et al. (2016) within *G. oceanica* and the additional one identified by us (M6) will prove to be evolutionarily independent, albeit difficult to diagnose morphologically. Resolution of this matter will be greatly enhanced by collection of additional samples from new areas within western Melanesia and application of extensive nuclear data. We recognize that our describing *G. corona* from this complex renders *G.* '*oceanica*' paraphyletic, but we take this action as a first step necessary toward resolving the taxonomy of this complex and to goad its further resolution by improved sampling and further studies. We demur from also describing lineage M6 at this time until additional data and more extensive samples from throughout Melanesia become available.

Although the trees illustrated in Tonione et al. (2016: figs 1, 3) were drawn as if rooted, in fact that study included no outgroups, so it could not be unambiguously determined that this complex originated in western Melanesia, as they postulated, though high molecular diversity there was certainly suggestive. We have rectified that shortage here by rooting our tree with two closely related *Gehyra* species (Heinicke et al., 2011) as outgroups, as well as the more distantly related *G. insulensis*, thereby placing the root of the *G. oceanica* group in western Melanesia. As well, Tonione et al. (2016) found that two of their molecular lineages (M3 and M5) overlap in geographic distribution, with both being found on New Britain (presence of both lineages M1 and P1 on several Pacific Islands may well be explained by recent human introductions). Our molecular results extend this observation of geographical overlap of deeply divergent lineages, with the earliest split in our tree separating clade [P1 + M5 + *G. corona*] from clade [M1 + M2 + M3 + M4 + M6] (Fig. 1). These clades widely overlap in geographical range in western Melanesia (Fig. 5, Tonione et al., 2016: fig. 1), further supporting western Melanesia as the source origin for the now-wide-ranging *G. oceanica* complex. Lastly, five of the eight lineages currently recognized in the *G. oceanica* complex are geographically restricted to western Melanesia. In sum, it appears that western Melanesia – and in particular the islands surrounding the Bismarck Sea – is the likely area from which the *G. oceanica* complex arose.

All genetic lineages identified by Tonione et al. (2016) and by us have their monophyly highly supported, but support values are less for the other internal branches in the tree, and in particular, the clade comprising (*G. corona* + P1 + M5) is not well resolved and forms what is functionally a polytomy (Fig. 1). Nonetheless, it remains clear that long isolation of lineages has led to deep genetic divergences among them and that biogeographic patterns among them are complex. It is to be hoped that future research involving nuclear data would provide greater resolution of these internal nodes and thereby increase confidence in the exact pattern of phylogenesis and biogeography in this complex.

The geographic range of *Gehyra corona* appears to be very limited. We searched nearby Sakar, Tolokiwa, and Umboi islands and found only *G. oceanica* lineage M6 (Fig. 5), which is sister to lineage M4, and sister to this clade were lizards of lineage M3 (Fig. 1), reported by Tonione et al. (2016) from nearby central New Britain and from the southern Solomon Islands. None of the M6 animals from Sakar, Tolokiwa, and Umboi islands has the distinctive colour-pattern dimorphism of *G. corona*, and they were quite divergent genetically (mean of 15%) from nearby *G. corona* even though Crown and Tolokiwa islands are only 60 km apart (Fig. 5). Other nearby islands in the Bismarck Volcanic Arc were not searched by us. Long Island is closely adjacent to Crown Island but was sterilized by a volcanic explosion of Krakatau-like intensity in the mid-1600s (Thornton, 2001); vertebrate surveys in 1999 failed to find any *Gehyra* (Cook et al., 2001), suggesting that a nocturnally conspicuous lizard like *G. corona* is not to be found there. It remains possible that *G. corona* will be found on small islands to the west (Bagabag, Karkar, Fig. 5). Specimens of *G. oceanica* from Karkar reside in the Australian Museum, Sydney, but these were unavailable for our examination; Bagabag has been poorly surveyed for reptiles and has only two reported lizards (Mys, 1988), and no *Gehyra* are known from there in collections. *Gehyra oceanica* remains to be reliably reported from New Guinea, with reports from that island (Bauer & Henle, 1994) typically being mis-identifications of congeners. Consequently, it currently seems likely that *G. corona* will be restricted to Crown Island, although broader surveys are required on other islands surrounding the Bismarck Sea that lie farther afield. Furthermore, considering the genetic divergence of *G. corona* from the other *G. oceanica* samples, and considering its very restricted range, additional deeply divergent genetic lineages of this complex may well be discovered with denser populational sampling across the many islands of western Melanesia.

We found *Gehyra corona* only in a small area on the eastern side of Crown Island, which is a steep, extinct, Quaternary volcanic cinder cone of 1475 ha and 566 m elevation (Johnson et al., 1972). However, we did not

survey more distantly along the coast because the steep terrain precluded easy access from our camp. If we are correct in our estimate that this species inhabits only low-elevation habitats near the coast, its total area of occupancy will be <1000 ha and possibly considerably less than this. Nonetheless, the island is mostly undisturbed rainforest because of its steep gradient. Johnson et al. (1972) noted that Crown Island was uninhabited at the time of their survey in September 1970. The current human population is small and seems restricted to a single small village on the eastern side of the island because it is the only place on the island with reliably accessible fresh water (via a shallow well). This is unlikely to change greatly because the island's unconsolidated ash does not allow for the persistence of streams. The dominant habitat on Crown Island is rainforest, though the coastal area in which we found *G. corona* consisted of disturbed secondary forest and open grassland (Fig. 6) containing many trees of *Cocos nucifera*, *Areca catechu*, and *Gliricidia sepium*, the last two introduced. So the species can clearly withstand modest amounts of habitat disturbance so long as trees remain present.

The limited range size of this species and its small estimated extent of occurrence might normally raise concerns about the conservation status of this species. However, the abundant habitat and difficulty for humans to inflict extensive habitat destruction on Crown Island because of the island's steep terrain and the low human population density make it unlikely that *G. corona* will be seriously threatened by human activities in the foreseeable future. The threat of volcanic sterilization of the island also seems remote inasmuch as Crown Island's volcano is extinct (Johnson et al., 1972) and the sterilization of adjacent Long Island did not remove *G. corona* from Crown Island. Hence, we consider this species' conservation status to be secure at this time.

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Appendix. Additional specimens examined

Gehyra oceanica – Caroline Islands: Pohnpei: Pingelap Atoll (BPBM 12563–68); Cook Islands: Rarotonga (BPBM 14963–65); Mariana Islands: Guam (UMMZ 129056–58); Papua New Guinea: Milne Bay Province: Woodlark Island (BPBM 39271–79, 39832–34); Society Islands: Moorea (BPBM 11064), Tahiti (BPBM 5865); Solomon Islands (UMMZ 99963).

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