

A new species of *Gehyra* Gray, 1834 (Squamata, Gekkonidae) from the Loyalty Islands and Vanuatu, and phylogenetic relationships in the genus *Gehyra* in Melanesia

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ABSTRACT

Geckos are one of the most widespread and diverse squamate taxa in the Pacific region and play a major role in explaining colonisation history and locating faunal affinities. We describe a new species of large growing *Gehyra* Gray, 1834 from the Loyalty Islands and Vanuatu based on molecular phylogenetics and morphology. *Gehyra georgpotthasti* n. sp. was formerly included within *G. vorax* Girard, 1857, but has longer postmental scales, more postrostral scales, and usually fewer subdigital lamellae and preloocal-femoral pores. We here designate a lectotype for *G. vorax* and propose a close relationship of this species to *G. georgpotthasti* n. sp. and *G. membranacruvalis* King & Horner, 1989. The phylogenetic position of *G. marginata* Boulenger, 1887 as sister

KEY WORDS

Gekkonidae,
Gehyra,
 Loyalty Islands,
 Vanuatu,
 Polynesia,
 16s rRNA,
 phylogeny,
 human-mediated
 dispersal,
 new species.

species to *G. oceanica* (Lesson, 1830) is described and new morphological evidence also disproves the previously supposed close relationship with *G. vorax*. Both *G. georgpotthasti* n. sp. and *G. vorax* have been introduced to Polynesia by human activities, as Polynesian populations of both taxa are genetically and morphologically indistinguishable from populations within their respective native ranges. But even within its native range, *G. georgpotthasti* n. sp. shows little genetic variability, inferring a recent colonisation history. Systematics of this group confirm the close zoogeographic relationship between Vanuatu and the Loyalty Islands.

RÉSUMÉ

Nouvelle espèce de Gehyra Gray, 1834 (Squamata, Gekkonidae) des îles Loyauté et du Vanuatu et relations phylogénétiques au sein du genre Gehyra en Mélanésie. Les geckos représentent l'un des groupes de reptiles squamates les plus diversifiés et les plus largement répartis dans la région du Pacifique. Ils contribuent amplement à notre connaissance de l'histoire des colonisations et des affinités de la faune. Nous décrivons ici une grande espèce de *Gehyra* Gray, 1834 des îles Loyauté et du Vanuatu sur la base de données obtenues à partir de la phylogénie moléculaire et de la morphologie. *Gehyra georgpotthasti* n. sp. était autrefois confondu avec *G. vorax* Girard, 1857, mais s'en distingue par des plaques post-mentales plus allongées, des écailles post-rostrales nombreuses et généralement moins de lamelles sous-digitales et de pores pré-cloacaux et fémoraux. Nous désignons ici un lectotype pour *G. vorax* et nous mettons en évidence ses affinités avec *G. georgpotthasti* n. sp. et *G. membranacuralis* King & Horner, 1989. La position phylogénétique de *G. marginata* Boulenger, 1887 comme espèce soeur de *G. oceanica* (Lesson, 1830) est décrite et de nouveaux critères morphologiques nous permettent de réfuter ses affinités avancées autrefois avec *G. vorax*. *Gehyra georgpotthasti* n. sp. et *G. vorax* ont été introduits en Polynésie par les activités humaines car les populations polynésiennes des deux taxons sont génétiquement et morphologiquement non différenciables des populations issues de leurs aires naturelles respectives. Toutefois, même dans son aire de répartition naturelle, *G. georgpotthasti* n. sp. ne présente que peu de variabilité génétique, semblant indiquer ainsi une colonisation récente. La systématique de ce groupe confirme les liens zoogéographiques importants entre le Vanuatu et les îles Loyauté.

MOTS CLÉS

Gekkonidae,
Gehyra,
 îles Loyauté,
 Vanuatu,
 Polynésie,
 16s rRNA,
 phylogénie,
 propagation
 anthropogénique,
 espèce nouvelle.

INTRODUCTION

Together with skinks, geckos represent the most widespread and diverse squamate taxon in the Pacific region (Gibbons 1985; Ineich & Blanc 1988; Adler *et al.* 1995; Allison 1996), resulting from their great dispersal abilities, biology (ecological generalists), size, and often commensal behavior facilitating human-mediated dispersal (Ineich & Blanc 1987; Dye & Steadman 1990; Case & Bolger 1991; Case *et al.* 1994), which has largely influenced current

distribution patterns (Fisher 1997; Austin 1999; Austin & Zug 1999). The Melanesian herpetofauna is generally thought to be of Papuan origin (Allison 1996), having colonised the Pacific islands via a stepping-stone route from New Guinea and surrounding large islands (Brown 1991; Hamilton *et al.* 2009). Although recent findings account for a major influence from New Caledonia and Australia to tropical south Pacific biotas (Keppel *et al.* 2009), these are not the source areas of Pacific islands reptiles. The Loyalty Islands have been considered as a link

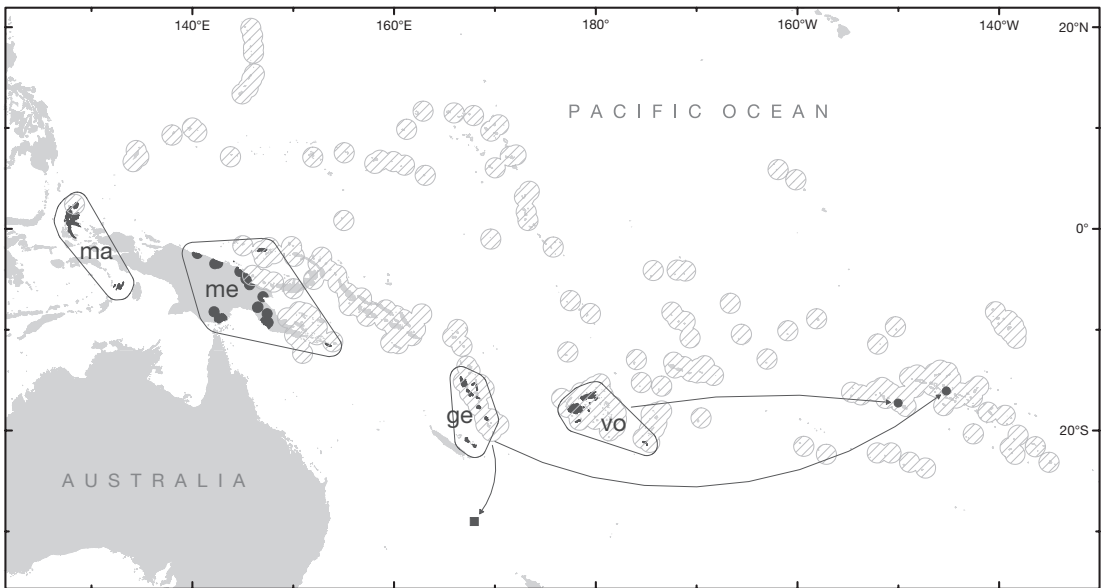


FIG. 1. — Distribution of giant *Gehyra* Gray, 1834 in the Pacific region: outlines delimit ranges of *G. marginata* Boulenger, 1887 (**ma**), *G. membranacuralis* King & Horner, 1989 (**me**), *G. georgpotthasti* n. sp. (**ge**), and *G. vorax* Girard, 1957 (**vo**); archipelagos, islands and regions with known occurrences are shaded black; arrows connect populations introduced to Polynesia (●) and the doubtful record from Norfolk Island (■) with their respective origins; grey hatched areas illustrate distribution of *G. oceanica* (Lesson, 1830).

between the Gondwana-derived New Caledonia and the rest of southern Melanesia (Roux 1913; Brown 1956; Bauer & Sadlier 2000; Hamilton *et al.* 2009) with great influences on specific composition from Vanuatu (Berlioz 1962; Bauer 1999; Ineich 2011). Much of the species richness in Vanuatu, however, has been suggested to originate from Fiji (Gibbons 1985). Regarding geckos, the Loyalty Islands are supposed to have a depauperate New Caledonian fauna (Bauer 1988), but also harbor typical Papuan taxa not present on New Caledonia, such as *Lepidodactylus* Fitzinger, 1843 group II species and *Gehyra* Gray, 1834 (Bauer & Vindum 1990; Ota *et al.* 1998; Ineich 2008, 2009).

The species-rich gekkonid genus *Gehyra* includes three large-growing species occurring in Melanesia: *G. marginata* Boulenger, 1887 from the Moluccas, *G. membranacuralis* King & Horner, 1989 from New Guinea, and *G. vorax* Girard, 1857 from southern Melanesia and introduced to the Polynesian Society Islands (Rösler & Obst 2007). A further morphological similar species, though smaller in size, is *G. oceanica* (Lesson, 1830), which

is widespread in the Pacific region (Fig. 1, see also Beckon 1992). Their considerable morphological similarity has caused some taxonomic confusion (Bauer & Henle 1994). Burt & Burt (1932) synonymised *G. vorax* with *G. oceanica* based on the presumably shared presence of dermal folds on the forelimb, which previously was considered as a major diagnostic feature of *G. vorax* (Boulenger 1885; De Rooij 1915). Still, most subsequent authors tentatively treated *G. vorax* as a separate taxon, mainly due to its much larger size compared to *G. oceanica* (e.g., Mertens 1974) and the fact that both forms often occur in sympatry (Zweifel 1980; Gibbons & Clunie 1984). Beckon (1992) showed that *G. vorax* is clearly distinct from *G. oceanica* by several morphologic characters and molecular phylogenetics suggest a closer relationship of *G. oceanica* with species from Southeast Asia, New Guinea and Micronesia (Sistrom *et al.* 2009; Oliver *et al.* 2010; Heinicke *et al.* 2011). Three different morphotypes of *G. vorax* have been defined: a Fiji-morphotype, a Vanuatu-morphotype and a New Guinea-morphotype (Beckon 1992). The latter

contains both *G. marginata* and *G. membranacruialis*, leading Beckon to synonymise these two species with *G. vorax*.

Giant *Gehyra* from Vanuatu and the Loyalty Islands were hitherto assigned to *G. vorax* (e.g., Boulenger 1885; Roux 1913; Sadlier & Bauer 1997) or more precisely, to the Vanuatu-morphotype (Beckon 1992). Herein, we provide morphological and genetic evidence that this Vanuatu-morphotype of *G. vorax* is a distinct species and discuss human translocation of this new species to Polynesia.

MATERIALS AND METHODS

DNA was extracted from muscle tissue using peqGOLD Tissue DNA Mini Kits (Peqlab). The primers 16sar-L (5' - CGC CTG TTT ATC AAA AAC AT - 3') and 16sbr-H (5' - CCG GTC TGA ACT CAG ATC ACG T - 3') of Palumbi *et al.* (1991) were used to amplify a section of the mitochondrial 16S ribosomal RNA gene. PCR cycling conditions are described by Schmitz *et al.* (2005). PCR products were purified using QIAquick PCR Purification Kits (Qiagen) and sequenced on an automatic sequencer. Sequences were checked with the original chromatograph data using the program PhyDE (Müller *et al.* 2007) and subsequently aligned with the MUSCLE algorithm (MUSCLE version 3.6, Edgar 2004). Alignment was refined manually if necessary. Additional sequences of *Gehyra* species and outgroups were obtained from GenBank, accession numbers of all sampled taxa are shown in Table 1. The final data set contains 21 taxa with 515 bp, from which 51 bp, representing one highly variable site of the 16s gene, could not be aligned unambiguously and thus were excluded from subsequent analyses. GTR+G was chosen as best-fitting model of nucleotide substitution by the Akaike Information Criterion using MrModeltest version 2.2 (Nylander 2004). Phylogenetic trees were computed with Maximum Likelihood and Bayesian Inference methods. Likelihood analysis with 2000 bootstrap replicates was conducted using the software PAUP* 4.0b10 (Swofford 2002). Bayesian analysis was done in MrBayes version 3.1 (Ronquist & Huelsenbeck 2003), using Markov

Chain Monte Carlo (MCMC) sets for 5×10^6 generations and sampled every 100 generations. The first 5×10^5 sampled trees were discarded as burn-in after empirically assessing the log-likelihood values of the sampled trees, and a 50% majority rule consensus was constructed from the remaining trees.

The morphology of a total of 60 specimens of *Gehyra marginata* and “*G. vorax*” was examined, including type material of the latter. Data for several metric, meristic, and categorical characters was compiled. Comparatively examined characters are snout-vent-length (from tip of snout to cloaca), tail length (from cloaca to tip of tail, only intact tails either completely original or with less than 10% regenerated), head width (at widest point), snout length (from tip of snout to anterior margin of orbit), snout width (distance between nostrils), orbit diameter (at widest point), orbit-ear distance (from posterior margin of orbit to anterior margin of ear opening), 4th toe width (at widest point), postmental ratio (width of postmental divided by its length), number of postrostral scales (all scales located between nasorostrals and rostral which are larger than cranial granules), numbers of subdigital lamellae under 3rd finger and under 4th toe (all scales at least twice as broad as long), number of supralabials, number of infralabials, number of precloacal-femoral pores in males (sum of both sides), subcaudal scalation (on non-regenerated parts of tail only), shape of tail section, toe webbing, dermal folds on limbs and trunk. Values for head length were calculated by summarising snout length, orbit diameter and orbit-ear distance. The threshold for adults was defined as the smallest – by means of the snout-vent length – specimen with visible precloacal-femoral pores. All measurements were taken with a digital calliper to the nearest 0.1 mm (snout-vent length and tail length to the nearest 1 mm) by the first author.

In addition, other materials were studied for comparison:

- *Gehyra marginata*: without locality, 2 specimens (ZFMK 66650, 66651); Moluccas, 4 specimens (ZFMK 78785-78788); Halmahera, 1 specimen (ZFMK 84308).
- *Gehyra oceanica*: Vanuatu, Pentecost, 1 specimen (MNHN 1894.0213); French Polynesia, Tuamotu,

TABLE 1. — Specimens used for genetic analyses.

Species	Collection no.	Locality	Reference	GenBank accession
<i>Gehyra georgpotthasti</i> n. sp.	ZFMK 91002	French Polynesia: Fakarava	This study	JN690003
<i>Gehyra georgpotthasti</i> n. sp.	ZFMK 91003	French Polynesia: Fakarava	This study	JN690004
<i>Gehyra georgpotthasti</i> n. sp.	ZFMK 91004	New Caledonia: Loyalty Islands: Dudun	This study	JN690002
<i>Gehyra georgpotthasti</i> n. sp.	MNHN 2009.0321	Vanuatu: Espiritu Santo	This study	JN690005
<i>Gehyra insulensis</i>	MNHN 2007.0098	French Polynesia: Vahanga	Rocha <i>et al.</i> 2009	FJ613471
<i>Gehyra insulensis</i>	–	Vanuatu: Torres Islands	Rocha <i>et al.</i> 2009	FJ613468
<i>Gehyra marginata</i>	ZFMK 78786	Indonesia: Moluccas	This study	JN689989
<i>Gehyra marginata</i>	ZFMK 78787	Indonesia: Moluccas	This study	JN689990
<i>Gehyra marginata</i>	ZFMK 78788	Indonesia: Moluccas	This study	JN689991
<i>Gehyra mutilata</i>	USNM 499244	Philippines: Luzon	Rocha <i>et al.</i> 2009	FJ613446
<i>Gehyra oceanica</i>	MNHN 2010.0622	Vanuatu: Espiritu Santo	This study	JN689992
<i>Gehyra oceanica</i>	MNHN 2010.0623	Vanuatu: Espiritu Santo	This study	JN689993
<i>Gehyra oceanica</i>	MNHN 2010.0624	Vanuatu: Espiritu Santo	This study	JN689994
<i>Gehyra oceanica</i>	MNHN 2010.0625	Vanuatu: Espiritu Santo	This study	JN689995
<i>Gehyra oceanica</i>	MNHN 2010.0626	Vanuatu: Espiritu Santo	This study	JN689996
<i>Gehyra oceanica</i>	MNHN 2010.0627	Vanuatu: Espiritu Santo	This study	JN689997
<i>Gehyra oceanica</i>	MNHN 2010.0628	Vanuatu: Espiritu Santo	This study	JN689998
<i>Gehyra oceanica</i>	MNHN 2010.0629	Vanuatu: Espiritu Santo	This study	JN689999
<i>Gehyra vorax</i>	ZFMK 91001	Fiji: Viti Levu	This study	JN690001
<i>Gehyra vorax</i>	ZFMK 91017	Fiji: Viti Levu	This study	JN690000
<i>Rhacodactylus auriculatus</i>	–	New Caledonia	Sound <i>et al.</i> 2006	DQ270584

Raraka, 1 specimen (USNM 5698); Marshall Islands, 1 specimen (ZFMK 20554); Australia, 4 specimens (ZFMK 20556–20559); western Samoa, 1 specimen (ZFMK 41074); Tonga, Eua, 10 specimens (ZFMK 41108–41115, 42047, 42050); Fiji, Viti Levu, 3 specimens (ZFMK 44721–44723); Palau, Kayangel Atoll, 2 specimens (ZFMK 45040, 45041). – *Gehyra vorax*: Fiji, 1 lectotype (USNM 5699/1), 1 paralectotype (USNM 5699/2), 2 specimens (MNHN 0000.5306, 1999.8283); Fiji, Viti Levu, 16 specimens (ZFMK 20553, 55268, 55269, 58195, 58196, 61853, 61854, 65514, 65516, 66567–66569, 68503, 68504, 91001, 91017); French Polynesia, Society Islands, 2 specimens (MTKD 8928, 8929).

ABBREVIATIONS

ANSP Academy of Natural Sciences, Philadelphia;
 MNHN Muséum national d'Histoire naturelle, Paris;
 MTKD Museum für Tierkunde, Dresden;
 NHMB Naturhistorisches Museum, Basel;
 USNM National Museum of Natural History, Washington D.C.;
 ZFMK Zoologisches Forschungsmuseum Alexander Koenig, Bonn;

RESULTS

Both phylogenetic methods produced trees with the same topology (Fig. 2). *Gehyra oceanica* forms a well-supported clade together with *G. marginata* from the Moluccas, while “*G. vorax*” constitutes another well-supported clade. High divergence is revealed within the latter, with a deep split between samples from Viti Levu (Fiji) and samples from Santo (Vanuatu), Dudun (Loyalty Islands) and Fakarava (French Polynesia) suggesting differences on species level between the Fijian and the other samples. Within the latter, divergence is very low and only resolved by ML analysis. Sequences from Dudun and Fakarava are identical. Uncorrected pairwise sequence distance between Fijian samples of “*G. vorax*” and the other localities is 5.7%, which is higher than the distance observed between the two morphologically distinct species *G. oceanica* and *G. marginata* (4%), but lower than the distance of 7.2% between *G. mutilata* (Wiegmann, 1834) and *G. insulensis* (Girard, 1857).

Morphological data for “*G. vorax*” (Table 2) are congruent with our phylogenetic results. We

TABLE 2. — Comparison of distinctive morphological characters of giant *Gehyra* spp. Metric characters taken from adult specimens only. Values for characters marked with an asterisk are given as percentages of snout-vent length.

	<i>Gehyra georgopotthasti</i> n. sp.			<i>Gehyra vorax</i>			<i>Gehyra marginata</i>		
	n = 31			n = 22			n = 7		
	mean	sd	range	mean	sd	range	mean	sd	range
Snout-vent length	112	± 13.4	82-142	137.2	± 13.2	109-155	133.8	± 5.6	130-142
Tail length*	75.3	± 6.0	67.8-84.9	65	± 6.0	57.9-72.5	77.5	± 8.9	71.2-83.8
Head length*	26.4	± 1.1	23.6-28.5	25.1	± 0.9	23.9-26.9	25.4	± 0.5	24.9-25.8
Head width*	21.7	± 1.2	19.4-24.3	20.6	± 1.0	19.2-22.5	19.8	± 0.4	19.4-20.2
Snout length*	12	± 0.6	10.9-13.3	11.6	± 0.6	10.6-12.6	11.4	± 0.5	11.1-11.9
Snout width*	3.3	± 0.3	2.7-3.6	3.3	± 0.4	2.4-3.9	2.9	± 0.3	2.6-3.2
Orbit diameter*	6.8	± 0.6	5.8-7.7	6.5	± 0.6	5.4-7.4	7.2	± 0.3	7.0-7.5
Orbit-ear distance*	7.6	± 0.5	6.7-9.0	7	± 0.5	6.3-7.8	6.8	± 0.4	6.5-7.2
4th toe width*	5.0	± 0.4	4.1-5.7	5.0	± 0.2	4.7-5.4	4.5	± 0.6	3.6-5.0
Postmental ratio	0.40	± 0.05	0.30-0.59	0.58	± 0.09	0.43-0.80	0.53	± 0.08	0.38-0.67
Postrostrals	3.8	± 1.3	2-6	1.3	± 0.5	1-2	1.4	± 0.8	1-3
Supralabials	14.1	± 1.4	12-17	14.1	± 1.1	12-16	13.7	± 1.2	12-15
Infralabials	12.8	± 1.4	10-16	12.3	± 0.7	11-14	13.2	± 1.3	11-15
Subdigital lamellae	22.8	± 1.7	20-28	27.3	± 1.8	23-32	24.9	± 1.3	23-27
3rd finger									
Subdigital lamellae	23.2	± 2.2	18-30	28.3	± 2.1	24-32	24.9	± 1.9	21-27
4th toe									
Precloacal-femoral pores	43.2	± 11.8	27-68	65.1	± 11.1	47-77	34.5	± 10.6	27-42
Subcaudals	median row of plate-like scales			median row of plate-like scales			subequal		
Tail section	rounded			rounded			flattened		
Toe webbing	up to half of toe length			up to half of toe length			up to half of toe length		
Dermal folds:									
Ante forelimb	from shoulder to base of toe			from shoulder to base of toe			from shoulder to base of toe		
Post forelimb	none			none			from pit to base of toe		
Lateral trunk	indistinct			distinct			broad, very distinct		
Ante hindlimb	none			none			from pit to base of toe		
Post hindlimb	from cloaca to base of toe			from cloaca to base of toe			from cloaca to middle of toe		

were able to discriminate two forms based on the characters listed above. One corresponds to the Fiji-morphotype as defined by Beckon (1992) and contains all specimens from Fiji, including the examined types of *G. vorax* (see below) and all genetically analysed Fijian specimens. Therefore, this form is considered to represent typical *G. vorax*. Two examples from the Society Islands (see Rösler & Obst 2007) also belong to this form. The second form comprises specimens from Vanuatu, the Loyalty Islands (New Caledonia) and Fakarava (Tuamotu Archipelago, French Polynesia), including all genetically analysed specimens from these localities, and is equal to Beckon's Vanuatu-morphotype. Specimens from the Moluccas fit the original description of *G. marginata*. They differ from the other forms in subcaudal scalation, shape

of the tail, and a more extensive development of the dermal folds.

According to Zug (1985), the type series of *G. vorax* contains three syntypes: USNM 5699/1, adult male; USNM 5699/2, adult female; and ANSP 7455, adult female. All were collected in Fiji during the United States Exploring expedition without specifying an island. A fourth specimen (USNM 5698) from Raraka in the Tuamotu Archipelago was attributed to the type series (Cochran 1961), but is not mentioned in the original description (Girard 1857). This locality was added in a subsequent publication, wherein an illustration of *G. vorax* is provided as well (Girard 1858a, b). Due to its later addition, this specimen must not be regarded as part of the type series in compliance with *The International Code of Zoological Nomenclature*, as already

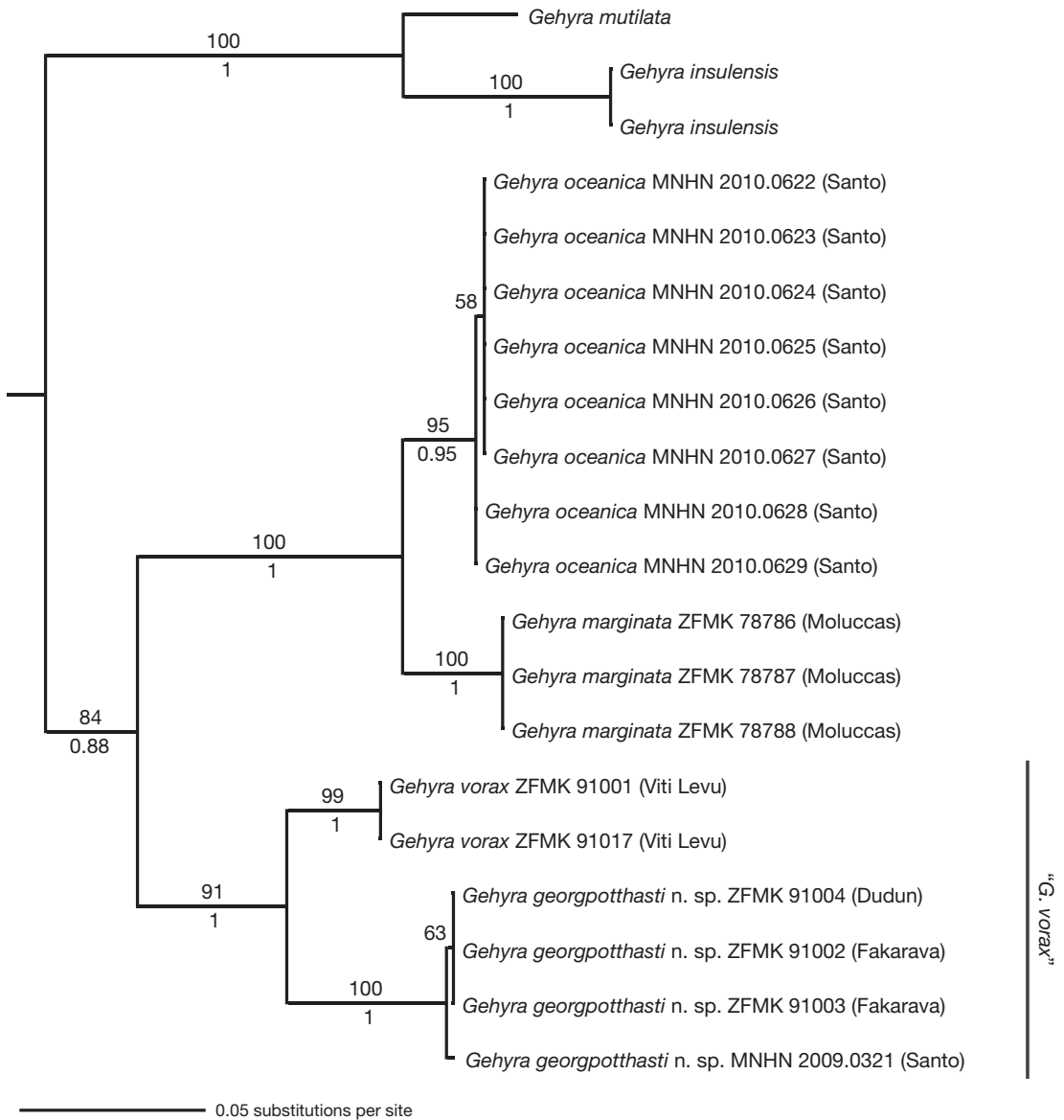


FIG. 2. — Maximum likelihood phylogram of Pacific *Gehyra* spp. based on sequences of the mitochondrial 16S rRNA gene. Likelihood bootstrap values are shown above branches, posterior probabilities below branches. Outgroup (*Rhacodactylus auriculatus* Bavay, 1869) not shown.

has been argued by Zug (1985). Furthermore, we identified USNM 5698 as a subadult *G. oceanica* (see also Crombie *in* Zug 1985), a species common on that atoll (Ineich & Blanc 1988). Girard's (1858b) illustration shows a male and thus can only refer

to specimen USNM 5699/1. We therefore designate USNM 5699/1 as the lectotype of *G. vorax* Girard, 1857. Consequently, the two remaining syntypes USNM 5699/2 and ANSP 7455 become paralectotypes.

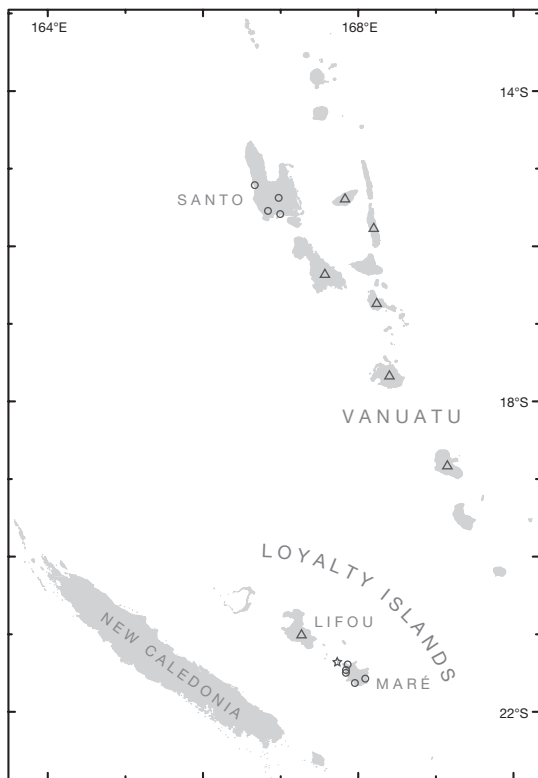


FIG. 3. — Detailed distribution of *Gehyra georgpotthasti* n. sp.: type locality (☆); other localities (○); islands only records (Δ). Localities for Loyalty Islands were compiled from museum specimens and data for Vanuatu from Ineich (2011).

SYSTEMATICS

Order SQUAMATA Oppel, 1811
 Family GEKKONIDAE Gray, 1825
 Genus *Gehyra* Gray, 1834

Gehyra georgpotthasti n. sp.
 (Figs 3-9)

Gehyra vorax – Boulenger 1883: 119. — Boulenger 1885: 153 (*partim*). — Strauch 1887: 29 (*partim*). — Roux 1913: 104. — De Rooij 1915: 45 (*partim*). — Baker 1928: 297. — Beckon 1992: 450 (*partim*). — Sadlier & Bauer 1997: 80. — Bauer & Sadlier 2000: 118. — Ineich 2011: 198.

TYPE MATERIAL. — Holotype: Loyalty Islands, Dudun Island, off the coast of Maré, 21°21'36"S, 167°43'48"E (Fig. 3), adult ♂, with hemipenes everted and tongue stuck out, F. W. Henkel (ZFMK 91004).

Paratypes (2 ♀♀, 4 ♂♂): same data as holotype, 2 adult ♀♀ (ZFMK 73578, 91018), adult ♂, with hemipenes everted (ZFMK 73902). — Vanuatu, Espiritu Santo, Butmas, 15°22'26.64"S, 166°58'27.42"E, 566 m asl, 2 adult ♂♂, with tails separated, 3.XII.2007, I. Ineich (MNHN 2007.0055, 0056). — Vanuatu, Espiritu Santo, Tasmate, 15°12'43.56"S, 166°39'38.05"E, subadult ♂, 9.XI.2006, I. Ineich (MNHN 2009.0321).

OTHER MATERIAL EXAMINED. — Vanuatu. Malakula, 3 specimens (MNHN 1894.0208-0210). — Pentecost, 4 specimens (MNHN 1894.0211, 0212, 0214, MNHN 1934.0054). — Epi, 3 specimens (MNHN 1974.1423, 1424, 1426). — Espiritu Santo, 1 specimen (MNHN 2010.0246). — Indetermined, 3 specimens (ZFMK 76990, 76991, 84310).

New Caledonia. Loyalty Islands, Maré, 7 specimens (NHMB 7029, 7031-7033, 7035, 7037, 7038). — Loyalty Islands, Lifou, 1 specimen (ZFMK 70455).

French Polynesia. Tuamotu, Fakarava, 2 specimens (ZFMK 91002, 91003).

DISTRIBUTION. — The species is currently known from many of the larger islands of Vanuatu where it does not extend further north than Espiritu Santo (Ineich 2011) and from Lifou and Maré (including the satellite islet Dudun) in the Loyalty Islands (Fig. 3). It has been introduced to Fakarava in the Tuamotu Archipelago, French Polynesia and probably also to Norfolk Island (Fig. 1, see discussion).

ETYMOLOGY. — This species is dedicated to Mr. Georg Potthast, in recognition of financial support for biodiversity research and nature conservation through the BIOPAT programme (www.biopat.de).

DIAGNOSIS. — A large (up to 142 mm from snout to vent), stoutly build gecko (Fig. 4) belonging to the genus *Gehyra*. Subdigital lamellae under the dilated portion of the toes are not longitudinally divided. Toes of *G. georgpotthasti* n. sp. are webbed up to about half of their length. Extensive dermal folds are present anterior of the forelimb and posterior of the hindlimb, spanning from shoulder to base of toe and from cloaca to base of toe, respectively. *Gehyra oceanica* has only slightly developed folds on limbs, which span directly between knee and elbow, and toes are only rudimentarily webbed. Furthermore, *G. oceanica* has fewer subdigital lamellae (max. 20, but usually less than 18 under 4th toe, compared to at least 18 in *G. georgpotthasti* n. sp.; see Table 2). Maximum snout-vent length of *G. oceanica* is smaller; in a series of 241 adult specimens from French Polynesia the largest was 93 mm (Ineich 1987), the by far largest specimen in the ZFMK collection is a male from western Samoa of 96 mm, and Beckon (1992) mentions 102 mm as maximum snout-vent length, whereas *G. georgpotthasti* n. sp. can grows up to 142 mm (see Table 2). *Gehyra oceanica* has at least 9-10 dark bands on tail (versus 5 to 6 such



FIG. 4. — Male holotype of *Gehyra georgpotthasti* n. sp. (ZFMK 91004) in life; total length of the specimen: 206 mm. Scale bars: 10 mm. Photographs: F. W. Henkel.

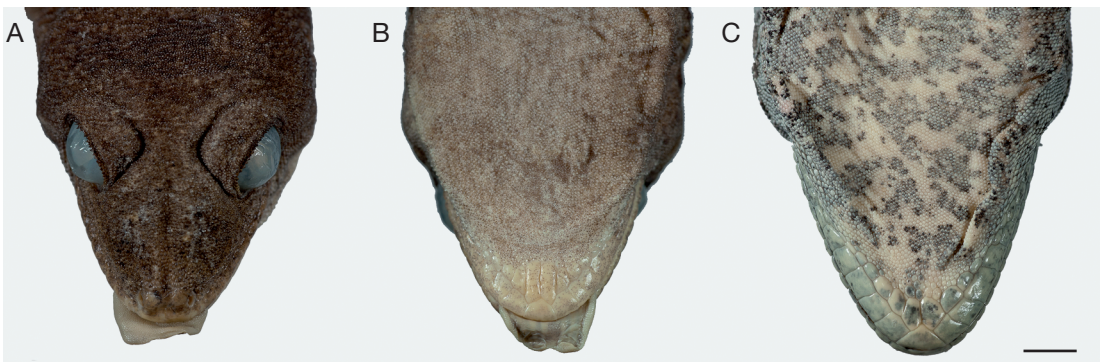


FIG. 5. — Scalation features on head: **A**, holotype of *Gehyra georgpotthasti* n. sp. (ZFMK 91004), dorsal view; **B**, same specimen, ventral view; **C**, *G. vorax* Girard, 1857 (ZFMK 55269), ventral view. Scale bar: 5 mm.

TABLE 3. — Measurements of examined specimens of *Gehyra georgpotthasti* n. sp. from the Loyalty Islands (L), Vanuatu (V), and the Tuamotu Archipelago (T).

	ZFMK 91004	ZFMK 73578	ZFMK 73902	ZFMK 91018	MNHN 2007.0055	MNHN 2007.0056	MNHN 2009.0321	ZFMK 70455	ZFMK 91002	ZFMK 91003
	L: Dudun				V: Santo: Butmas		V: Santo: Tasmate	L: Lifou	T: Fakarava	
	male	female	male	female	male	male	male	male	male	female
Sex	115	97	132	104	137	142	112	127	112	90
Snout-vent length										
Tail length	91	69	–	–	–	–	–	–	–	61
Head length	30.1	26.3	34.1	27.1	32.3	35.1	28.3	33.1	30.7	–
Head width	26.3	20.8	27.2	22.0	28.1	30.7	24.0	24.7	25.5	–
Snout length	13.0	12.2	14.9	12.6	14.9	16.4	13.2	14.3	13.5	–
Snout width	3.9	3.5	4.6	3.5	4.0	4.4	3.9	3.8	4.0	–
Orbit diameter	8.6	7.0	9.9	6.9	8.0	8.5	7.0	9.8	7.9	–
Orbit-ear distance	8.5	7.1	9.3	7.6	9.4	10.2	8.1	9.0	9.3	–
4th toe width	6.1	4.7	6.4	4.3	6.6	6.8	5.6	5.6	5.7	4.1
Postmental ratio	0.30/0.35	0.38/0.41	0.44/0.41	0.39/0.34	0.44/0.37	0.50/0.43	0.33/0.33	0.38/0.35	0.38/0.33	0.39/0.41
Postrostrals	3	4	2	6	3	3	4	3	5	3
Supralabials	13/12	16/14	14/13	14/13	13/13	15/15	17/13	13/14	15/12	–/13
Infralabials	14/14	11/11	12/11	14/13	12/13	12/12	14/15	12/12	12/14	13/12
Subdigital lamellae	23/22	23/23	26/26	21/20	23/23	28/25	22/–	21/–	23/24	20/22
3rd finger										
Subdigital lamellae	21/22	22/22	30/30	22/23	22/23	25/24	24/25	22/26	22/22	21/21
4th toe										
Precloacal-femoral pores	63	0	68	0	45	43	47	40	35	0

bands in *G. georgpotthasti* n. sp.). Subcaudal scalation of *G. georgpotthasti* n. sp. consists of enlarged, plate-like scales arranged in a median row, whereas *G. oceanica* and *G. marginata* have subequal scales or multiple (two or three) median rows of slightly enlarged, nearly subequal scales. *Gehyra marginata* also differs in having a flattened rather than rounded tail in section and has distinct dermal folds posterior of the forelimb and anterior of the hindlimb, both are merged with a broad fold along trunk. *Gehyra membranacruralis* lacks dermal folds on forelimb. *G. vorax* differs in shape of postmentals (short vs elongated in *G. georgpotthasti* n. sp.) and postrostral scale numbers (up to two vs. two or more in *G. georgpotthasti* n. sp.). Morphological characters of *G. georgpotthasti* n. sp. and similar species are summarised in Table 2.

DESCRIPTION

Holotype

Snout-vent length 115 mm. Forehead has a median groove extending from between nostrils to below

eyes. Dorsocranial scalation uniform, consisting of small granular scales. Supralabials are 14 and 13, left and right respectively; infralabials are 14 on each side. Rostral shield possesses a median suture and two further sutures originating from corner of posterior indentation of the rostral. Two scales are embedded into this indentation. These are posteriorly bordered by a single, large internasal (Fig. 5). Nostril bordered by rostral shield, 1st supralabial, nasorostral (as large as 1st supralabial), and three postnasals (two to four times larger than surrounding granules). Mental shield pentagonal, slightly smaller than 1st infralabials. Postmentals about three times longer than wide, twice as long as the mental, and reaching into gular granules (Fig. 5). Infralabials bordered by a series of scales larger than other gular scales, but diminishing in size posteriorly from postmentals.

TABLE 3. — Continuation.

	NHMB 7029	NHMB 7031	NHMB 7032	NHMB 7033	NHMB 7035	NHMB 7037	NHMB 7038	ZFMK 76990	ZFMK 76991	ZFMK 84310
	L: Maré: Padaoua		L: Maré: Médou		L: Maré: Pénélo			V: without precise locality		
	male	female	male	male	female	female	female	male	male	female
Sex										
Snout-vent length	102	99	120	112	111	102	125	114	116	114
Tail length	80	—	84	—	—	—	—	86	—	—
Head length	27.2	26.6	32.4	30.0	29.9	28.2	30.7	30.4	30.9	28.8
Head width	23.3	21.8	28.6	25.1	25.4	24.8	26.9	23.0	23.1	23.3
Snout length	13.0	13.2	14.4	13.6	13.8	13.3	13.8	13.0	13.7	13.2
Snout width	3.6	3.6	4.1	3.9	3.8	3.7	4.1	3.2	3.1	3.6
Orbit diameter	6.2	6.2	7.2	7.5	7.0	6.8	7.6	8.5	8.7	8.0
Orbit-ear distance	8.0	7.2	10.8	8.9	9.1	8.1	9.3	8.9	8.5	7.6
4th toe width	5.2	5.0	6.8	6.4	5.8	5.7	6.2	5.1	5.1	5.4
Postmental ratio	0.41/0.41	0.39/0.32	0.40/0.33	0.35/0.38	0.33/0.33	0.38/0.38	0.40/0.35	0.41/0.40	0.41/0.44	0.42/0.42
Postrostrals	5	5	6	5	4	2	2	4	—	4
Supralabials	13/13	14/13	13/13	13/12	13/14	13/12	15/15	14/14	12/12	15/15
Infralabials	13/12	12/12	10/11	12/12	13/13	12/12	13/13	11/11	10/10	14/15
Subdigital lamellae 3rd finger	21/23	21/23	20/24	22/23	23/23	23/22	22/21	23/24	24/24	—/24
Subdigital lamellae 4th toe	25/24	25/21	21/23	22/24	24/23	23/21	22/21	21/23	26/27	26/24
Preloacal-femoral pores	54	0	39	54	0	0	0	32	27	0

63 preloacal-femoral pores arranged in a W-shaped line (Fig. 6). Three clustered preloacal tubercles on each side of tail base. Original tail 91 mm long and subcircular in section. Tail dorsally whorled, with longitudinally ten scales per whorl, which are about twice as large as granules on back. Subcaudal scales arranged in one median row of enlarged plates, these sometimes with a median suture (Fig. 7).

Fingers and toes broad, with webbing that extends to about half the toe length between 3rd and 4th toe. Subdigital lamellae undivided, counting 23 on left 3rd finger, 22 on right 3rd finger, 21 on left 4th toe, and 22 on right 4th toe. First finger without claw, but a rudimentary sheath is present. First toe bears a small terminal claw. Remaining fingers and toes with large claws on free phalanges.

Dermal folds present, well-developed anterior of the forelimb, spanning from shoulder to base of

1st finger, and posterior of the hindlimb, spanning from cloaca to base of 5th toe (Fig. 6).

Colouration in ethanol is brownish-grey on the dorsal side, with faint darker patches. Ventral side off-white with very fine freckles, flanks more or less mottled with brown. Colouration in life was brown with five dark brown saddle patches between forelimbs and base of tail. Head, tail and flanks also with dark patches (Fig. 4). Ventral side light brown with a yellow hue, which becomes more intense in preloacal region. Iris brown.

Variation

Detailed data on morphometric and meristic characters of this species are presented in Table 3. Noteworthy variation was observed in the number of subdigital lamellae, of which can be to 30 under the 4th toe as in one paratype (ZFMK 73902) and the number of male preloacal-femoral pores, which

TABLE 3. — Continuation.

	MNHN 1894. 0208	MNHN 1894. 0209	MNHN 1894. 0210	MNHN 1894. 0211	MNHN 1894. 0212	MNHN 1894. 0214	MNHN 1934. 0054	MNHN 1974. 1423	MNHN 1974. 1424	MNHN 1974. 1426	MNHN 2010. 0246
	V: Malakula			V: Pentecost				V: Epi		V: Santo	
Sex	male	female	juvenile	male	male	juvenile	male	male	male	male	juvenile
Snout-vent length	113	100	69	114	82	70	106	114	101	122	64
Tail length	—	—	—	—	—	—	90	—	—	—	49
Head length	29.5	27.1	19.6	30.7	23.4	19.4	28.6	31.4	27.0	32.7	16.0
Head width	23.5	21.3	14.3	26.3	17.8	14.1	24.7	24.4	21.8	26.5	13.1
Snout length	12.9	12.3	9.1	14.0	10.5	8.6	13.0	14.6	12.1	14.8	7.1
Snout width	3.8	3.6	2.6	3.9	2.5	2.8	3.5	3.9	3.1	3.6	2.4
Orbit diameter	7.7	6.8	5.2	7.2	6.2	5.5	7.1	8.1	7.5	8.8	4.9
Orbit-ear distance	8.9	8.0	5.3	9.5	6.7	5.3	8.5	8.7	7.4	9.1	4.0
4th toe width	5.8	5.2	2.9	5.9	3.8	2.9	5.0	6.4	4.6	6.9	2.5
Postmental ratio	0.47/0.41	0.40/0.38	0.37/0.37	0.38/0.37	0.48/0.48	0.46/0.46	0.44/0.45	0.33/0.33	0.55/0.59	0.38/0.38	0.42/0.33
Supralabials	15/16	15/15	15/15	16/16	15/16	13/14	17/17	16/15	13/12	15/16	12/14
Infralabials	14/12	15/15	13/14	16/15	14/15	13/12	14/14	14/13	13/13	13/12	11/13
Subdigital lamellae	22/23	-/22	21/19	24/23	24/23	-/18	24/25	-/26	21/22	23/23	23/25
4th toe											
Precloacal-femoral pores	48	0	0	58	38	0	35	28	34	32	0

range from 27 to 68 (43 to 68 in paratypes). Number and shape of postrostral scales is very variable, often asymmetrical, but generally consisting of two or more scales located between the rostral and the two nasorostrals and more-or-less larger than cranial granules. Postmental scalation is uniform with little variation compared to the holotype.

Colouration is variable, mostly consisting of brown and grey, but yellow, reddish or olive elements are not uncommon. The tail has five to six dark bands, which are especially distinct in juveniles and less distinct or even absent in adults. On Santo, there is a “red” (Fig. 8) and an “ornated” morph (Fig. 9). The first shows a similar colouration to that described for the holotype, but has reddish elements on the dorsum. The ornated morph has the dorsal saddle patches dissolved and shows light and dark ocella-like patches on greyish-brown ground.

Besides the precloacal-femoral pores, which are only present in males, there are no differences between sexes concerning scalation. According to our data, males grow larger than females: the

largest male specimen (MNHN 2007.0056) has a snout-vent length of 142 mm, mean value of all examined males with visible pores is 115 mm; the largest female (NHMB 7038) measures 125 mm, mean value of all adult females is 105 mm.

REMARKS

Predominantly nocturnal and arboreal, occupying habitats in rainforest and along beaches. At Dudun, the species, however, dwells on coconut trees and screwpines (*Pandanus*). Inactive specimens were observed during daytime hiding in between dead leaves of *Pandanus*. Specimens from Maré were collected on coconut trees (Roux 1913).

Eggs obtained from a captive specimen originating from Dudun (ZFMK 91018) are hard-shelled, spherical, and measure 16.0-16.5 × 17.4-18.8 mm (n = 3). Eggs from Santo range from 16.59-18.11 × 18.59-19.75 mm (n = 3; Ineich 2011). Beckon (1992) mentions egg lengths of 17.2 mm (Maré) and 15.8 mm (Espiritu Santo). For comparison, eggs of *G. vorax* from Viti Levu are 18.6-19.4 × 19.4-



FIG. 6. — Preloacal region and dermal folds of the holotype (ZFMK 91004) of *Gehyra georgopotthasti* n. sp. Scale bar: 10 mm. Photograph: F. W. Henkel.



FIG. 7. — Subcaudal scalation at mid portion of the tail: **A**, holotype of *Gehyra georgopotthasti* n. sp. (ZFMK 91004); **B**, *G. vorax* Girard, 1857 (ZFMK 55269); **C**, *G. marginata* Boulenger, 1887 (ZFMK 84308); **D**, *G. oceanica* (Lesson, 1830) from Fiji (ZFMK 44722). Scale bar: 5 mm.

20.4 mm ($n = 3$). Gibbons & Zug (1987) report egg sizes of 18×20 mm from the same island. A hatchling out of an egg from Santo measured 41 mm in snout-vent length and 39 mm in tail length.

It is worth mentioning that two specimens, MNHN 2007.0055 from Santo and ZFMK 91002 from Fakarava, had part of their skin damaged when captured, revealing conspicuously green coloured

muscle tissue on shoulder and neck (Fig. 8). We did not observe this feature in other specimens, but this is mostly owing to the fact that the colouration does not persist in alcohol. A specimen of *G. vorax* photographed at Viti Levu has damaged its skin at the same body part, but no greenish colouration is visible. So far, we have no explanation for the biological function of green muscle tissue.

DISCUSSION

TAXONOMIC CONSEQUENCES

Our findings largely support the previously defined morphotypes of *Gehyra vorax* of Beckon (1992) and confirm its specific distinctiveness from *G. oceanica*. Nevertheless, from adding more morphological characters and genetic information we conclude that these morphotypes actually represent different species. As a result, typical *G. vorax* (i.e. the Fiji-morphotype) are restricted to Fiji and Tonga (Fig. 1; see Zug 1991 and Morrison 2003 for detailed distribution in Fiji). The Tonga specimen, if really from there, could not be examined by us, but was placed into the Fiji-morphotype by Beckon (1992). Further evidence can be drawn from parasitological studies, which detected different species of pterygostomatid mites hosted by *G. georgpotthasti* n. sp. in Vanuatu and by Fijian *G. vorax* (Bertrand & Ineich 1986, 1987).

Although they were mentioned in the original description (Boulenger 1887) and by other authors (e.g., De Rooij 1915), Beckon (1992) ignored the diagnostic characters of *G. marginata* (i.e. flattened tail, dermal folds along trunk and between limbs), misleading him to synonymise it with his New Guinea-morphotype, which corresponds to *G. membranacuralis* (Beckon 1992; Bauer & Henle 1994). Specimens from New Guinea were not available to us for examination, but based on the data given by King & Horner (1989), *G. membranacuralis* is clearly different from *G. marginata* in the above mentioned characters. We therefore consider *G. membranacuralis* to be valid and closely allied to *G. georgpotthasti* n. sp. and *G. vorax*. This assumption is based on morphology, but supported by previous molecular studies, which suggested a distant relationship between *G. membranacuralis* and *G. oceanica* (Sistrom *et al.* 2009; Oliver *et al.* 2010). On the other hand, molecular analyses clarified the phylogenetic position of *G. marginata*, which is not found within the clade comprising *G. vorax*, but turned out to be the sister species of *G. oceanica* (Heinicke *et al.* 2011). This makes “*G. vorax*” *sensu* Beckon (1992) paraphyletic. Thus, the specific status of *G. marginata* is confirmed. A morphological hint to the close relationship of

G. oceanica and *G. marginata* revealed by molecular phylogenetics is the subcaudal scalation, which is similar in both species in the absence of the enlarged, plate-like scales present in *G. georgpotthasti* n. sp. and *G. vorax*. Some authors have reported *G. oceanica* to possess such enlarged subcaudals (Bauer & Sadlier 2000; Morrison 2003), but an examination of several specimens in the collections of the MNHN and ZFMK from different localities throughout Melanesia and Polynesia showed that *G. oceanica* has either subequal sized scales or two to three median rows of only slightly enlarged scales under the tail, just as observed in *G. marginata*. Single enlarged scales were only found in the regenerated parts of tails or, occasionally, intermixed with double or triple rows. This corroborates our assumption that “*G. vorax*” *sensu* Beckon (1992) consists of three distinct and allopatric species, and that *G. marginata* represents another, separate species more closely allied to *G. oceanica*.

BIOGEOGRAPHY

Specimens of *G. georgpotthasti* n. sp. from Dudun and Lifou constitute the first records of *Gehyra* for these islands. Dudun is a satellite islet of Maré, where the most recent records were made 100 years ago (Roux 1913). The record from Norfolk Island (Boulenger 1885) has been argued to be in error (Cogger *et al.* 1983; Bauer & Sadlier 2000). The biotic break within Vanuatu (Hamilton *et al.* 2010) does not apply for *Gehyra*, as *G. georgpotthasti* n. sp. occurs on islands in north (Santo, Ambae, Pentecost, Malakula, Epi, Efate) and south (Erromango) of Cheesman’s Line.

Divergence of *G. georgpotthasti* n. sp. within their native range seems relatively low, given that we analysed the two most distant populations. Sequences of specimens from Santo to the north and Dudun near Maré in the south only differ in 0.4%. It has been suggested that low intraspecific divergences in some skink species in eastern Melanesia and Polynesia are the result of human-mediated dispersal, whereas higher divergences indicate natural dispersal over a longer timespan (Austin 1999; Austin & Zug 1999). Low intraspecific divergence has also been detected in both *G. mutilata* and *G. insulensis* (Rocha *et al.* 2009), inferring a relatively recent



FIG. 8. — Adult male of *Gehyra georgpotthasti* n. sp. (paratype MNHN 2007.0055), red colour morph from Santo, note the green muscle tissue on shoulder where skin is shred. Photograph: I. Ineich.

expansion of the distributional ranges most probably supported by human translocations. Unlike *G. mutilata* and *G. oceanica*, *G. georgpotthasti* n. sp. and *G. vorax* are not commensal generalists, but rather forest-dwelling specialists (Zug 1991; Beckon 1992; Henkel 1995; Ineich 2011). This reduces the chance of human translocation (Ineich 2010), and is mirrored by the wider distributional range of the commensal species, which are present on many remote Pacific islands (Ineich & Blanc 1987, 1988; Beckon 1992; Bauer & Henle 1994; Fisher 1997). Both Vanuatu and the Loyalty Islands are considered to be of younger geological age than surrounding archipelagos, having emerged 2 and 1.8 Mya, respectively (Kroenke & Rodda 1984; Greene & Wong 1988; Kroenke 1996; Bauer & Sadlier 2000). So, with either mode of dispersal, Vanuatu and the Loyalty Islands were presumably colonised not long ago in geological time scales, which could explain the low level of intraspecific genetic divergence. Sequence divergence between *G. vorax* from Fiji and *G. georgpotthasti* n. sp. is moderate and suggests a young split between these two species. Nevertheless, these differences consist



FIG. 9. — Adult male of *Gehyra georgpotthasti* n. sp. (paratype MNHN 2007.0056), ornated colour morph from Santo. Photograph: I. Ineich).

of specific character state combinations, which can be considered as autapomorphies. The islands' young age has also been suggested as an explanation for the low number of endemic reptiles compared to adjacent archipelagos like New Caledonia, Fiji and the Solomons (Bauer 1999; Hamilton *et al.* 2009).

Despite its low distance from New Caledonia, the Loyalty Islands share most of their herpetofauna with smaller Pacific islands and archipelagos (Solomons, Vanuatu, and Fiji), rather than with New Caledonia. Many of its gekkonid species are absent from New Caledonia, probably because of competition with diplodactylids, an ancient lineage of geckos. The systematics of *Gehyra* reflect a close zoogeographic relationship between Vanuatu and the Loyalty Islands, as both share the same species, *G. georgpotthasti* n. sp. With the sister species *G. vorax* occurring on Fiji, the herpetofaunal affinities to this archipelago are also confirmed. Although several authors list "*G. vorax*" for the Solomon Islands (Gibbons & Clunie 1984; Bauer & Henle 1994; Bauer & Sadlier 2000), which would function as the major stepping-stone to colonise Vanuatu and Fiji from New Guinea, voucher specimens are still lacking (McCoy 2006). The group is also absent from the Torres Islands (Ineich 2009) located between the Solomons and Vanuatu, yet hitch-hiking and probable extinctions in source areas or on stepping-stones might obscure interpretations of current diversity patterns (Keppel *et al.* 2009). An alternative hypothesis would be that the group has colonised Fiji and Vanuatu independently from a continental source and not via adjacent archipelagos, as has been shown in spiders (Gillespie 2002). However, colonisation history of the group remains unclear and further studies incorporating molecular data for New Guinean species, especially *G. membranacuralis*, are needed.

HUMAN TRANSLOCATION

The occurrence of both *G. georgpotthasti* n. sp. and *G. vorax* in Polynesia, several thousand kilometers away from their native ranges (Fig. 1), raises the question how they have reached these remote islands. Even though transoceanic dispersal is not unusual in geckos (e.g., Gamble *et al.* 2008), the fact that *G. georgpotthasti* n. sp. from the Loyalty Islands

shares the same haplotype with specimens from Polynesia infers a very recent dispersal, without leaving time for any sequence evolution since dispersal. Intensive field surveys made by one of us (II) in French Polynesia from 1985 to 1990 have failed to find any sign of that species or its typical eggs (Ineich 1987). Morphologically, specimens from Fakarava and the Society Islands (without precise locality) are also indistinguishable from *G. georgpotthasti* n. sp. and *G. vorax*, respectively (see also Rösler & Obst 2007), and constitute the first and only records of these species from French Polynesia. Anthropogenic translocation seems to be the most plausible explanation for the remote occurrences, and has been reported for other gecko species in the Pacific (e.g., Case *et al.* 1994). Fakarava is a small atoll with atoll adapted vegetation and no rainforest, yet *G. georgpotthasti* n. sp., like *G. vorax*, is mostly a humid forest species (Ineich 2011). Thus, the species most probably was introduced very recently, but cannot reproduce. The vouchers of *G. vorax* from the Society Islands date back to 1890, without a rediscovery since then despite recent field work, which substantiates our assumption that there are no reproductive populations of *G. georgpotthasti* n. sp. or *G. vorax* in Polynesia. Reconsidering introduction as an explanation for those isolated occurrences of *Gehyra* spp., *G. georgpotthasti* n. sp. might as well have reached Norfolk Island (see above), but was not able to become established or went extinct due to the lack of suitable habitat (Beckon 1992).

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and background of the expedition, see Bouchet *et al.* (2011a), and for a review of the geography and natural history of Santo, see Bouchet *et al.* (2011b). II wishes to thank Rufino Pineda for his support during the 2007 Torres Islands visit which was made possible through funding from MNHN (programme “État et structure de la biodiversité actuelle et fossile”). Finally he thanks Ms. Donna Kalfatak of the Environment Unit of the Republic of Vanuatu who provided valuable support to conduct our research in Vanuatu and all the inhabitants of the village of Tasmate for their unforgettable hospitality. FWH is indebted to the authorities of Fiji and New Caledonia for issuing permits to collect and export specimens.

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