

Gastrointestinal helminth communities of two gekkonid lizard species, *Nactus multicarinatus* and *Nactus pelagicus* (Squamata: Gekkonidae), from the Republic of Vanuatu, Oceania

Stephen R. Goldberg^{a*}, Charles R. Bursey^b, Alison M. Hamilton^c
and Christopher C. Austin^d

^aDepartment of Biology, Whittier College, Whittier, CA 90608, USA; ^bDepartment of Biology, Pennsylvania State University, Shenango Campus, Sharon, PA 16146, USA; ^cDepartment of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA; ^dDepartment of Biological Sciences, 119 Foster Hall, Louisiana State University, Baton Rouge, LA 70803, USA

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Gastrointestinal helminth communities of two gekkonid species, *Nactus multicarinatus* and *Nactus pelagicus*, from the Vanuatu Archipelago were examined. Both helminth communities were depauperate: *N. multicarinatus* harboured one species of Digenea, *Mesocoelium monas*, one species of Cestoda, *Oochoristica javaensis*, four species of Nematoda, *Hedruris hanleyae*, *Parapharyngodon maplestoni*, *Physocephalus* sp. (larvae in cysts), Filarioidea gen. sp. (juvenile); *N. pelagicus* harboured one species of Cestoda, *O. javaensis*, four species of Nematoda, *H. hanleyae*, *Falcaustra tannaensis*, *P. maplestoni*, *Physocephalus* sp. (larvae in cysts). In each helminth community *P. maplestoni* represented a core species and *H. hanleyae* was a secondary species. It is postulated that the helminth fauna infecting lizards of the Vanuatu Archipelago originated in Australia and Papua New Guinea and reached the archipelago by rafting; their establishment in Vanuatu was fortuitous.

Keywords: *Nactus multicarinatus*; *Nactus pelagicus*; helminths; Vanuatu; Oceania

Introduction

Oceans are the most effective barriers to the distribution of terrestrial organisms (Cox and Moore 2010). For non-volant organisms, dispersal to islands lacking a history of mainland connection results from the chance combination of favourable winds and the presence of floating vegetation. The probability of arrival, much less subsequent establishment, is extremely low (Cox and Moore 2010). One would therefore predict that lizards on small oceanic islands would have a markedly depauperate helminth fauna. This was found to be the case in a recent survey of helminths in *Emoia caeruleocauda* from the Mariana Islands (Goldberg et al. 2011). To further test this hypothesis, we examined the helminth communities of two species of gekkonid lizards, the Pacific slender-toed gecko, *Nactus multicarinatus* (Günther 1872), and the pelagic gecko, *Nactus pelagicus* (Duméril 1858), from the Vanuatu Archipelago, Oceania. Both are medium-sized, primarily terrestrial geckos. Adults of *N. pelagicus* range from 48 to 65 mm snout–vent length (Zug 1991) and adult *N. multicarinatus* have an average

*Corresponding author. Email: sgoldberg@whittier.edu

snout–vent length of 60 mm (McCoy 2006). *Nactus multicaarinatus* occurs in New Guinea, the Solomon Islands, northeastern Australia and the Vanuatu Archipelago; *N. pelagicus* is found in Fiji, the Loyalty Islands, New Caledonia, Micronesia, Tonga, Niue, Samoa, Tuvalu and southern Vanuatu (Eckstut et al. 2009). The islands of southern Vanuatu encompass the region of overlap in the distribution of these two species.

Vanuatu is an 83-island archipelago of volcanic origin (Figure 1); most of the islands are mountainous, with a tropical or sub-tropical climate (International Business Publications 2009). In addition to the two species of *Nactus*, the lizard fauna includes 10 other species of geckos: *Gehyra mutilata*, *Gehyra oceanica*, *Gehyra vorax*, *Gekko vittatus*, *Hemidactylus frenatus*, *Lepidodactylus buleli*, *Lepidodactylus*

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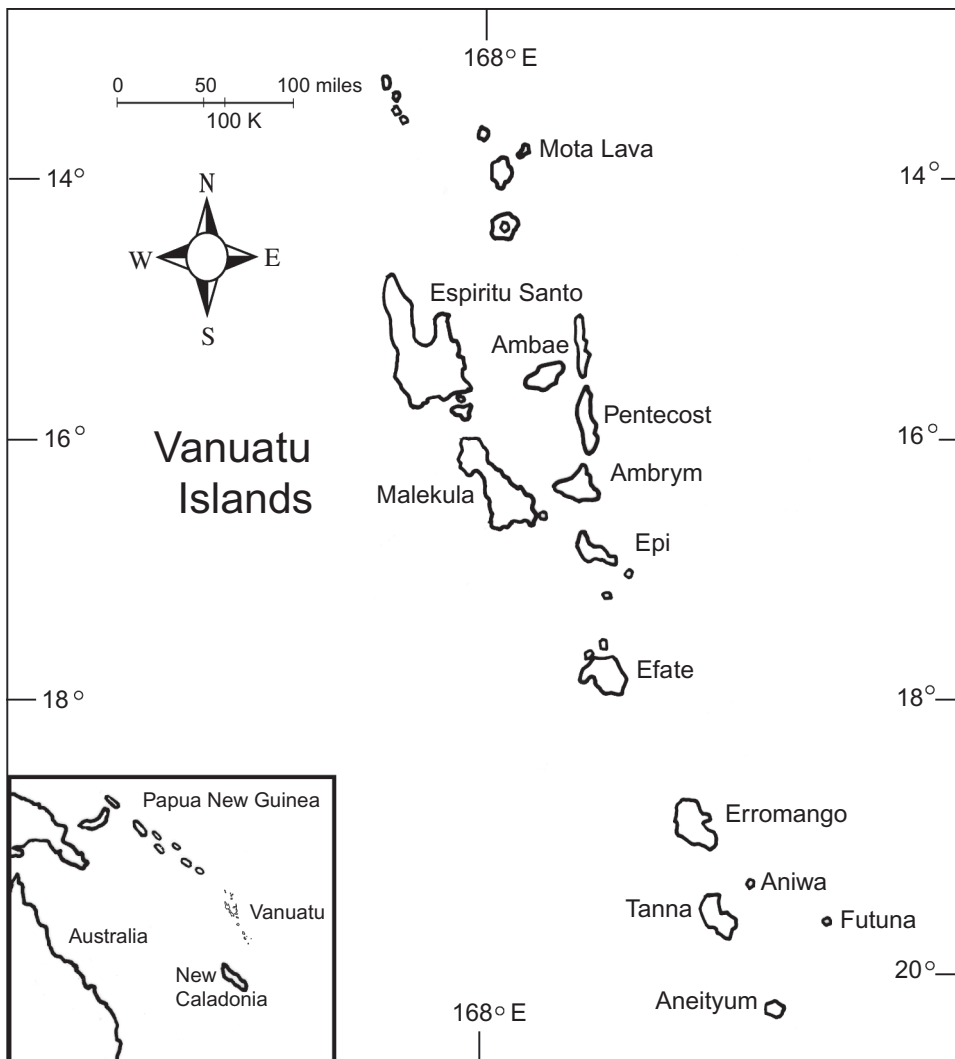


Figure 1. Vanuatu Archipelago; islands from which *Nactus* were collected.

guppyi, *Lepidodactylus lugubris*, *Lepidodactylus vanuatuensis* and *Perochirus guentheri* (Ota et al. 1998; Ineich 2008, 2009; Hamilton et al. 2009, 2010). Vanuatu also has a diverse assemblage of skinks, the majority of which are in the genus *Emoia*: *E. aneityumensis*, *E. atrocostata*, *E. caeruleocauda*, *E. cyanogaster*, *E. cyanura*, *E. erronan*, *E. impar*, *E. nigra*, *E. nigromarginata* and *E. sanfordi* (Hamilton et al. 2008, 2009). The remainder of the lizard fauna consists of three other skink species (*Caledoniscincus atropunctatus*, *Cryptoblepharus novohebridicus*, *Lipinia noctua*) and the introduced iguana, *Brachylophus bulabula* (Keogh et al. 2008; Hamilton et al. 2009, 2010).

Materials and methods

A total of 165 *N. multicaarinatus* and 172 *N. pelagicus* collected from Vanuatu, Oceania during 2000, 2001, 2004 and 2005 by A.M.H. and deposited in the herpetology collection at the Louisiana State University, Museum of Natural Science (LSUMZ), Baton Rouge, LA, USA, were examined for helminths (Appendix 1). Geckos were collected by hand, examined within 24 hr of capture, then preserved in 10% neutral-buffered formalin and stored in 70% ethanol. Visceral organs were removed and sent to Whittier College for helminthological examination. The oesophagus, stomach and large and small intestines were examined under a dissecting microscope. Digeneans and cestodes were regressively stained in haematoxylin, mounted in Canada balsam and examined under a compound microscope. Nematodes were cleared in glycerol on a microscope slide, covered with a cover slip and studied under a compound microscope.

Parasite community terminology is in accordance with Bush et al. (1997). Parasite community similarity was measured using Sorenson's quotient of similarity (Q/S) and Morisita's index (Brower et al. 1998). Voucher helminths were deposited in the United States National Parasite Collection (USNPC), Beltsville, MD (Appendix 2).

Results

We found one species of Digenea, *Mesocoelium monas* (Rudolphi, 1819); one species of Cestoda, *Oochoristica javaensis* Kennedy, Killick and Beverley-Burton, 1982; five species of Nematoda, *Falcaustra tannaensis* Bursey, Goldberg, Hamilton and Austin, 2010; *Hedruris hanleyae* Bursey and Goldberg, 2000; *Parapharyngodon maplestoni* Chatterji, 1933; *Physocephalus* sp. (larvae in cysts); Filarioidea gen. sp. (juveniles). The core helminth in the parasite communities of both *N. multicaarinatus* and *N. pelagicus* was *P. maplestoni* (Tables 1, 2). *Hedruris hanleyae* was also found at high levels of intensity and prevalence in both *N. multicaarinatus* (Table 1) and *N. pelagicus* (Table 2). *Hedruris hanleyae* has the broadest distribution within Vanuatu; this species was found in *Nactus* from all islands surveyed except Ambae. Likewise, *P. maplestoni* is widely distributed in Vanuatu and infected *Nactus* from all islands surveyed except Ambae and Erromango.

Patterns of parasite infection differed between *N. multicaarinatus* and *N. pelagicus*. The highest mean intensity of infection in *N. multicaarinatus* was caused by *P. maplestoni* (Table 1); in *N. pelagicus* the highest mean intensity of infection was caused by *H. hanleyae* (Table 2). *Parapharyngodon maplestoni* was the most prevalent

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Table 1. Samples from islands showing number (N), prevalence (P), mean intensity \pm 1 SD ($\bar{x} \pm$ SD) and range for helminths from 165 *Nactus multicaarinatus* from Vanuatu, Oceania.

n	<i>Mesocoelium monas</i>		<i>Oochoristica javaensis</i>		<i>Hedruris hanleyae</i>		<i>Parapharyngodon maplextoni</i>		<i>Physoccephalus</i> sp.		Filarid gen. sp.		
	N	P	N	P	N	P	N	P	N	P	N	P	
	($\bar{x} \pm$ SD, range)		($\bar{x} \pm$ SD, range)		($\bar{x} \pm$ SD, range)		($\bar{x} \pm$ SD, range)		($\bar{x} \pm$ SD, range)		($\bar{x} \pm$ SD, range)		($\bar{x} \pm$ SD, range)
Ambae	6	0	0	0	0	0	0	0	0	0	0	0	0
Ambrym	23	1 4%	19 48%	(1.7 \pm 1.0, 1-4)	39 48%	(3.5 \pm 3.2, 1-11)	72 57%	(5.5 \pm 4.6, 1-17)	0	0	0	0	0
Efate	22	0	1 5%	(1.0)	2 9%	(1.0)	15 27%	(5 \pm 1.2, 1-4)	0	0	0	0	0
Epi	17	0	2 12%	(1.0)	12 29%	(2.4 \pm 3.1, 1-8)	32 65%	(2.9 \pm 1.9, 1-5)	0	0	0	0	0
Espiritu Santo	22	0	0	(1.0)	46 41%	(5.1 \pm 8.7, 1-28)	98 91%	(7.3 \pm 1.6, 1-34)	5 18%	5 18%	5 18%	0	0
Malakula	22	0	1 4%	(1.0)	12 35%	(1.5 \pm 0.8, 1-3)	36 52%	(3.0 \pm 0.18, 1-6)	0	0	0	0	0
Mota	27	1 4%	39 61%	(2.8 \pm 2.1, 1-7)	27 61%	(1.9 \pm 0.92, 1-4)	109 83%	(5.7 \pm 3.4, 2-15)	61 39%	61 39%	61 39%	0	0
Lava	(1.0)	0	0	(1.0)	23 46%	(1.8 \pm 0.93, 1-4)	56 77%	(2.8 \pm 2.2, 1-8)	(6.8 \pm 7.1, 1-24)	(6.8 \pm 7.1, 1-24)	(6.8 \pm 7.1, 1-24)	3 8%	3 8%
Pentecost	26	0	0	(1.0)	0	0	0	0	56 77%	56 77%	56 77%	(1.5 \pm 0.71, 1-2)	(1.5 \pm 0.71, 1-2)
		N = 2	N = 62	N = 161	N = 418	N = 85	N = 3						

Table 2. Samples from islands showing number (*n*), helminth prevalence (P), mean intensity \pm 1 SD ($\bar{x} \pm$ SD) and range for 172 *Nactus pelagicus* from Vanuatu, Oceania.

	<i>Oochoristitica javaensis</i>		<i>Hedruris hanleyae</i>		<i>Falcaustra tannaensis</i>		<i>Parapharyngodon maplestoni</i>		<i>Physocephalus</i> sp.	
	<i>n</i>	$\bar{x} \pm$ SD, range)	<i>N</i>	<i>P</i> (x \pm SD, range)	<i>N</i>	<i>P</i> (x \pm SD, range)	<i>N</i>	<i>P</i> (x \pm SD, range)	<i>N</i>	<i>P</i> (x \pm SD, range)
Aneityum	10	0	5	10% (5.0)	0	0	8	50% (1.6 \pm 0.55, 1-2)	0	0
Aniwa	23	0	112	87% (5.6 \pm 4.5, 1-19)	0	0	33	57% (2.5 \pm 1.4, 1-5)	1	4% (1.0)
Erromango	5	0	2	20% (2.0)	0	0	0	0	0	0
Futuna	5	0	7	40% (3.5 \pm 0.71, 3-4)	0	0	2	20% (2.0)	0	0
Tanna	129	4	22	4% (4.4 \pm 3.8, 1-10)	15	4% (3.0 \pm 2.8, 1-8)	417	87% (3.8 \pm 2.5, 1-11)	223	5% (31.9 \pm 79.4, 1-212)
			<i>N</i> = 4	<i>N</i> = 148	<i>N</i> = 15	<i>N</i> = 460			<i>N</i> = 224	

helminth parasite of *N. multicarinatus* from all islands where parasites were recovered (Table 1). In contrast, the most prevalent helminth parasite of *N. pelagicus* varied among islands (Table 2). *Parapharyngodon maplestoni* was most prevalent in *N. pelagicus* from the islands of Aneityum and Tanna, whereas *H. hanleyae* was most prevalent in *N. pelagicus* from the islands of Aniwa, Erromango and Futuna.

Discussion

Three of the helminth species found in this study, *Mesocoelium monas*, *Oochoristica javaensis* and *Parapharyngodon maplestoni*, have wide distribution patterns. *Mesocoelium monas* is almost cosmopolitan, found in all areas except the Nearctic (Goldberg et al. 2009) and has been reported in 12 species of New Guinean skinks (Goldberg et al. 2010a). The distribution of *Oochoristica javaensis* is somewhat controversial (see Bursey et al. 2005) but the species is known to occur in geckos and skinks from Malaysia and Papua New Guinea (Goldberg et al. 2008, 2010a, b) as well as in geckos from Oceania (Goldberg and Bursey 2002). *Hedruris hanleyae* was described from the gecko *Hemidactylus garnotii* from the Cook Islands, Oceania (Bursey and Goldberg 2000) and has been reported from 14 species of skinks and seven additional species of geckos from Oceania (Bursey and Goldberg 2001; Goldberg and Bursey 2002; Goldberg et al. 2005, 2008). *Hedruris hanleyae* has been previously reported in five species of skinks from Vanuatu (Goldberg et al. 2005) but has not previously been reported from *N. multicarinatus* or *N. pelagicus*. The recently described *Falcaustra tannaensis* is known only from Vanuatu; it is the first species of this genus from Oceania but has congeners in Australia and Papua New Guinea (Bursey et al. 2010). We could not identify the filarioid juveniles found in *N. multicarinatus* from the island of Pentecost; however, *Icosiella papuensis* Johnston, 1967 and *Ochoterella papuensis* Johnston, 1967 occur in Papua New Guinea, while five species of *Oswaldofilaria*, two species of *Piraturboides* and one species of *Pseudothamagudia* are known from Australia (Baker 1987). Therefore, there are several taxa that occur in the region and might be expected to have colonized the islands of Vanuatu.

To become established, immigrant parasites must find a suitable habitat and host. Although the life cycles of most of the helminths found in this study have not been examined, life cycle studies of congeners are available. Members of the Pharyngodonidae, such as *P. maplestoni*, have direct (monoxenous) life cycles and infection most probably occurs when contaminated substrate is ingested as lizards forage for food (Anderson 2000). Consequently, a colonizing *P. maplestoni* needs only to find a suitable habitat. This lack of dependence on an intermediate host is likely to increase the efficacy of *P. maplestoni* at colonizing new environments, and probably contributes to the broad distribution of this species across the Vanuatu archipelago, as well as the high prevalence and intensity of this helminth in *Nactus*.

In contrast to *P. maplestoni*, the other helminth species identified from these two species of *Nactus* require intermediate hosts. Species of *Mesocoelium* have a single molluscan host; cercariae emerge from the sporocyst to encyst in the viscera of the mollusc or occasionally leave the molluscan host to encyst on vegetation (Prudhoe and Bray 1982). *Nactus* could become infected by ingestion of an infected snail or vegetation containing cysts. Several helminth genera found in this study use invertebrates as part

of their life cycle. Some species of *Oochoristica* use beetles as intermediate hosts (Conn 1985). Species of *Hedruris* require an intermediate host (Hasegawa and Otsuru 1979), and the Filarioidea are transmitted by haematophagous arthropods (Anderson 2000). Species of *Falcaustra* are thought to develop to the third stage outside the primary host and then invade various invertebrates, which serve as paratenic hosts (Anderson 2000). Infection by *Physocephalus* most probably occurred after human settlement of the islands, as adults of *Physocephalus* typically occur in the stomachs of wild and domestic pigs and dung beetles serve as intermediate hosts (Anderson 2000). *Nactus* probably become infected with helminths by ingesting infected invertebrates. Although there is no published study of the diet of *N. multicaarinatus* and *N. pelagicus*, arthropods and beetles have been observed in the stomach contents of both species in Vanuatu. In Vanuatu, both species of *Nactus* are commonly found on moist soils under limestone, piles of stones, and in areas where coconut husks have been piled during copra production; large numbers of isopods, snails and a variety of invertebrates are readily found in these habitats and probably form the bulk of the diet of these geckos (A.M. Hamilton unpublished data).

Roca (1993) suggested that the prevalence of encysted larval nematodes may indicate the importance of lizards in food webs because lizards can serve as transport hosts; alternatively, the presence of encysted larval nematodes may only indicate the importance of beetles as a food item to lizards.

As defined by Bush et al. (1997), a component community consists of the parasites of a host species. The two component communities in this study are different. There were six helminth species in the *N. multicaarinatus* component community and five helminth species in the component community of *N. pelagicus*. There were seven helminth species in total, but only four in common. Sorenson's quotient of similarity (Q/S) is based on the species presence in a community and for this study equals 72.7 (Q/S ranges from 0, no species in common, to 100, all species in common). The difference between the two component communities results from the absence of *Falcaustra tannaensis* in the component community of *N. multicaarinatus* and the absence of *Mesocoelium monas* and filarioids in the component community of *N. pelagicus*. Whether the difference in species diversity is because of the small sample size or represents a lack of helminth immigration cannot be determined from the available data. The Morisita index (I_M) is based on number of individuals as well as species diversity and for this study equals 0.96 (I_M ranges from 0, no similarity, to 1, identical). The reason for the greater similarity using the Morisita index is that 79% of the individuals in the component community of *N. multicaarinatus* and 71% of the individuals in the component community of *N. pelagicus* belong to the same two helminth species, *H. hanleyae* and *P. maplestoni*. These two helminth species are the predominant helminth species found in this study.

Helminths have been classified as core and secondary species according to their prevalence (P): species with prevalences > 30% are deemed to be core species; species with 10–30% prevalence are considered to be secondary species (Roca 1993). In both component communities, *P. maplestoni* is a core species (P = 79, *N. multicaarinatus*; P = 71, *N. pelagicus*) and *H. hanleyae* is a secondary species (P = 22, *N. multicaarinatus*; P = 17, *N. pelagicus*). It is interesting to note the prevalence of larvae of *Physocephalus* sp. (P = 12, *N. multicaarinatus*; P = 26, *N. pelagicus*), a species that does not mature in poikilotherms, but that is often found in cysts in the stomach wall of vertebrates.

The gastrointestinal helminth fauna of the two species of *Nactus* that occur in Vanuatu consists of one species of Digenea (*Mesocoelium monas*), one species of Cestoda (*Oochoristica javaensis*), and five species of Nematoda (*Falcaustra tannaensis*, *Hedruris hanleyae*, *Parapharyngodon maplestoni*, *Physocephalus* sp., and unidentified Filarioidea). Before this study, *H. hanleyae* was known to occur in five species of skinks collected from the island of Efate in Vanuatu (Goldberg et al. 2005). This study highlights a difference between the helminth communities found in different families of lizards from Vanuatu. *Parapharyngodon maplestoni* is the core species of the component parasite communities of both *N. multicaarinatus* and *N. pelagicus*, and occurs in *N. multicaarinatus* collected from the island of Efate; this species was absent from all five species of scincid lizards examined from Efate (Goldberg et al. 2005). *Hedruris hanleyae* was found in all skinks examined from Efate, but only two individuals of this species were observed in the 22 *N. multicaarinatus* from Efate examined in our study. These data suggest that ecological or habitat differences between the skink and gecko faunas of Vanuatu may influence the relative importance of specific helminth species in the supracommunity.

Differences in the helminth communities of *N. multicaarinatus* and *N. pelagicus* could result from two primary causes: (1) differences in the ecology or habitat use between the two gecko species or (2) differences in the helminth populations within the source populations of *N. multicaarinatus* and *N. pelagicus* that colonized Vanuatu. It seems unlikely that the dissimilarity we identified results from variation between the species in habitat use or diet, because both species are forest floor dwellers that are commonly found on moist soils under piles of rocks, stones, vegetation and coconut husks (Zug 1991; McCoy 2006), and stomach contents of the two species appear similar (A.M. Hamilton, unpublished data). Variation between the helminth faunal communities of the source populations of *N. multicaarinatus* and *N. pelagicus* might explain the disparity in the component helminth communities of these species in Vanuatu. The colonization of Pacific oceanic islands by reptiles has been suggested to have occurred by means of a stepping stone route from New Guinea into the islands of the southwest Pacific (Brown 1991; Allison 1996). *Nactus multicaarinatus* has a distribution that includes the Solomon Islands and New Guinea, it seems plausible that infected lizards colonizing Vanuatu were originally from New Guinea and reached Vanuatu by rafting. All of the helminth species found in the Vanuatu *N. multicaarinatus* populations are known from New Guinea lizards. *Nactus pelagicus*, on the other hand, is distributed throughout Oceania and is absent from the hypothesized source of much of the lizard fauna of the oceanic Pacific islands. Perhaps the source population of the Vanuatu *N. pelagicus* is Oceania; the greater importance of *H. hanleyae* seen in some Vanuatu populations of *N. pelagicus* is concordant with the Oceania-wide distribution of this helminth species.

There is a contrast between the large lizard helminth faunas in New Guinea (Goldberg et al. 2008, 2010a, b) and the small number of species we report from *Nactus* on Vanuatu. This disparity might suggest that the rate of lizard immigration to oceanic islands is low and perhaps this host population bottleneck drives a similar bottleneck in parasite diversity. It should be noted, however, that the parasite faunas reported here only represent two closely related, ecologically similar species. It is possible that an investigation of additional species of lizards from Vanuatu might reveal a more diverse assemblage of parasite species.

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Appendix 1. *Nactus multicaarinatus* and *Nactus pelagicus* from Vanuatu deposited at the Louisiana State University, Museum of Natural Science (LSUMZ) and examined for helminths by island

Ambae: *Nactus multicaarinatus* ($n = 6$) LSUMZ 90692, 90694–90697, 90701.
Ambrym: *Nactus multicaarinatus* ($n = 23$) LSUMZ 90933, 90985–91003, 91018, 91026, 91038.
Aneityum: *Nactus pelagicus* ($n = 10$) LSUMZ 90462–90465, 90472–90475 90478, 90479).
Aniwa: *Nactus pelagicus* ($n = 23$) LSUMZ 90869, 90870, 91187, 91189–91208.
Efate: *Nactus multicaarinatus* ($n = 22$) LSUMZ 90794–90798, 90801, 90802, 90805–90808, 90811–90816, 90819–90823.
Epi: *Nactus multicaarinatus* ($n = 17$) LSUMZ 90824, 90827–90838, 90840–90843.
Erromango: *Nactus pelagicus* ($n = 5$) LSUMZ 90489–90493.
Espiritu Santo: *Nactus multicaarinatus* ($n = 22$) 90767, 90768, 90770–90775, 90777–90782, 90784–90787, 90790–90792.
Futuna: *Nactus pelagicus* ($n = 5$) LSUMZ 90482–90486.
Malakula: *Nactus multicaarinatus* ($n = 22$) LSUMZ 91048, 91053–91063, 91066, 91067, 91069, 91070–91073, 91075–91077.
Mota Lava: *Nactus multicaarinatus* ($n = 23$) LSUMZ 90646–90660, 90665, 90666, 90668, 90670, 90672–90675.
Pentecost: *Nactus multicaarinatus* ($n = 26$) LSUMZ 90713, 90715–90717. 90719, 90721, 90731–90750.
Tanna: *Nactus pelagicus* ($n = 130$) LSUMZ 90442–90448, 90499–90514, 90517–90536, 90538, 90540–90559, 90571–90591, 90594–90597, 906700–90604, 90606, 90609–90619, 90621–90628, 90631, 90633, 90635, 90859–90870.

Appendix 2. Voucher helminths from *Nactus multicaarinatus* and *Nactus pelagicus* from Vanuatu, Oceania deposited in the United States National Parasite Collection (USNPC).

Nactus multicaarinatus: *Mesocoelium monas*, Ambryn, (USNPC 103751); *Oochoristica javaensis*, Efate (USNPC 103752); *Hedruris hanleyae*, Ambryn (USNPC 103753), Efata (USNPC 103754), Epi (USNPC 103755), Espiritu Santo (USNPC 103756), Malakula (USNPC 103757), Mota Lava (USNPC 103758), Pentecost (USNPC 103759); *Parapharyngodon maplestoni*, Ambryn (USNPC 103760), Efate (USNPC 103761), Epi (USNPC 103762), Espiritu Santo (USNPC 103763), Malakula (USNPC 103764), Mota Lava (USNPC 103765), Pentecost (USNPC 103766); *Physocephalus* sp. (larva in cyst), Pentecost (USNPC 103767).
Nactus pelagicus: *Oochoristica javaensis*, Tanna (USNPC 103768); *Hedruris hanleyae*, Aneityum (USNPC 103769), Aniwa (USNPC 103770), Erromango, (USNPC 103771), Fortuna (USNPC 103772), Tanna (USNPC 103773); *Falcaustra tannaensis*, Tanna (USNPC 102768–102770); *Parapharyngodon maplestoni*, Aneityum (USNPC 103774), Aniwa (USNPC 103775), Futuna (USNPC 103776), Tanna (USNPC 103777); *Physocephalus* sp. (larva in cyst), Tanna (USNPC 103767).