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Gastrointestinal Helminths in *Nactus* spp. (Squamata:
Gekkonidae) from Six Papua New Guinean Islands

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Errata

In the previous print issue of *Pacific Science* (44.4, October 2020, pp. 381–387) the appendices are missing from the article “Gastrointestinal Helminths in *Nactus* spp. (Squamata: Gekkonidae) from Six Papua New Guinean Islands” by Stephen R. Goldberg, Charles R. Bursey, and Fred Kraus.

APPENDIX 1

Nactus Specimens from Papua New Guinea
Islands Examined from the Herpetology
Collection of the Bishop Museum (BPBM),
Honolulu, Hawaii, USA

Bougainville Island: BPBM 16984–17000.
Fergusson Island: BPBM 15854–15860,
15862–15870, 15872–15884. **Misima Island:**
BPBM 16739–16758, 19823–19828. **New
Britain Island:** BPBM 22010, 22012,
22013, 22015, 22017–22023, 22025–22029,
22031, 22032. **Rossel Island:** BPBM 19857–
19875, 19880. **Sudest Island:** BPBM 19830,
19831, 19833, 19834, 19836, 19837, 19839–
19842, 19844–19849, 19852, 19854.

APPENDIX 2

Harold W. Manter Parasite Collection
(HWML), University of Nebraska, Lincoln,
USA) Accession Numbers for Helminths
from *Nactus* sp. Collected (by island) in Papua
New Guinea Examined from the Herpetology
Collection of the Bishop Museum (BPBM),
Honolulu, Hawaii, USA

Bougainville: *Aplectana zweifeli* (HWML
111607); *Cosmocerca zugii* (HWML 111608);
Rictulariidae gen. sp. (larva) (HWML
111609).

Fergusson: *Sauracanthorhynchus sphe-
nomorphicola* (HWML 111610); *A. zweifeli* (HWML
111611); *Bakeria bakeri* (HWML 111612);
C. zugii (HWML 111613); *Parapharyngodon
maplestoni* (HWML 111614); *Abbreviata* sp.
(larva) (HWML 111615); Rictulariidae gen.
sp. (larva) (HWML 111616).

Misima: *Mesocoelium brevicacum* (HWML
111617); *Gekkotaenia novaeguineensis*
(HWML 111618); *S. sphe-
nomorphicola* (HWML 111619); *A. zweifeli* (HWML
111620); *B. bakeri* (HWML 111621); *C. zugii*
(HWML 111622); *Meteterakis crombiei*
(HWML 111623); *P. maplestoni* (HWML
111624); *Physalopteroides milnensis* (HWML
111625); *Abbreviata* sp. (larva) (HWML
111626); Rictulariidae gen. sp. (larva)
(HWML 111627).

New Britain: *G. novaeguineensis* (HWML
111628); *A. zweifeli* (HWML 111629);
M. crombiei (HWML 111630); *P. maplestoni*
(HWML 111631); *Abbreviata* sp. (larva)
(HWML 111632); Rictulariidae gen. sp.
(larva) (HWML 111633).

Rossel: *G. novaeguineensis* (HWML
111634); *S. sphe-
nomorphicola* (HWML
111635); *A. zweifeli* (HWML 111636);
B. bakeri (HWML 111637); *C. zugii* (HWML
111638); *M. crombiei* (HWML 111639);
P. maplestoni (HWML 111640); *Abbreviata*
sp. (larva) (HWML 111641); Rictulariidae
gen. sp. (larva) (HWML 111642).

Sudest: *S. sphe-
nomorphicola* (HWML 111644);
A. zweifeli (HWML 111645); *P. maplestoni*
(HWML 111646); *Abbreviata* sp. (larva)
(HWML 111647); Rictulariidae gen. sp.
(larva) (HWML 111648).

APPENDIX 3

List of Helminths with BPBM Number for
Nactus spp. from Six Islands from Papua New
Guinea Examined from the Herpetology
Collection of the Bishop Museum (BPBM),
Honolulu, Hawaii, USA. Numbers with no
parasite have ——— behind them.

Bougainville (*n* = 17)

BPBM number: Helminths

16984: 2 *Aplectana zweifeli*; 16985: ———;
16986: ———; 16987: ———; 16988: —;
16989: ———; 16990: 3 *A. zweifeli*; 16991:
———; 16992: 9 Rictulariidae gen. sp.
(larvae), 3 *A. zweifeli*, 1 *Cosmocerca zugii*;
16993: ———; 16994: ———; 16995:
———; 16996: ———; 16997: ———;
16998: ———; 16999: ———; 17000: 1 *A.
zweifeli*.

Fergusson (*n* = 29)

15854: ———; 15855: 3 *A. zwei-
feli*, 1 *C. zugii*; 15856: 4 *Abbreviata* sp. (larva), 3
A. zweifeli; 15857: 2 *A. zweifeli*; 15858: 1
Bakeria bakeri, 6 *A. zweifeli*, 7 *C. zugii*; 15859: 1
Abbreviata sp. (larva), 2 *B. bakeri*, 1 *C. zugii*, 5
A. zweifeli; 15860: 3 *A. zweifeli*, 1 *C. zugii*;
15862: 7 Rictulariidae gen. sp. (larvae), 3

Parapharyngodon maplestoni; 15863: 17 Rictulariidae gen. sp. (larvae), 13 *P. maplestoni*; 15864: 1 *P. maplestoni*; 15865: 8 *A. zweifeli*; 15866: 3 *P. maplestoni*; 15867: 4 *P. maplestoni*; 15868: 4 *P. maplestoni*; 15869: 1 *P. maplestoni*, 1 *Mesocoelium breviaecum*; 15870: 1 *P. maplestoni*; 15872: 1 *A. zweifeli*, 1 *Sauracanthobrychus spheonomorphicola*; 15873: 1 *C. zugii*, 7 *A. zweifeli*; 15874: 1 *S. spheonomorphicola*, 1 *C. zugii*, 17 *A. zweifeli*; 15875: 1 *B. bakeri*, 1 *C. zugii*, 4 *P. maplestoni*, 4 *A. zweifeli*; 15876: 1 *P. maplestoni*, 21 *A. zweifeli*; 15877: 4 *B. bakeri*, 6 *A. zweifeli*; 15878: 1 *S. spheonomorphicola*, 1 *B. bakeri*, 45 *A. zweifeli*; 15879: 8 *Abbreviata* sp. (larva), 5 *S. spheonomorphicola*; 15880: 1 *Abbreviata* sp. (larva), 11 *P. maplestoni*; 15881: 5 *P. maplestoni*, 1 *B. bakeri*; 15882: 4 *P. maplestoni*; 15883: 3 *S. spheonomorphicola*, 3 *P. maplestoni*; 15884: 4 *P. maplestoni*, 1 *B. bakeri*.

Misima ($n = 26$)

16739: ———; 16740: 1 *P. maplestoni*, 10 *A. zweifeli*; 16741: 5 *P. maplestoni*; 16742: 1 *Gekkotaenia novaeguineanaensis*, 8 *P. maplestoni*, 6 *A. zweifeli*; 16743: 1 *S. spheonomorphicola*, 4 *P. maplestoni*, 1 *A. zweifeli*; 16744: 1 *Abbreviata* sp. (larva), 8 *P. maplestoni*; 16745: 22 Rictulariidae gen. sp. (larvae), 8 *A. zweifeli*, 2 *P. maplestoni*; 16746: 3 *P. maplestoni*, 2 *A. zweifeli*; 16747: 6 *Abbreviata* sp. (larva), 1 *C. zugii*, 9 *A. zweifeli*, 5 *Meterakis crombiei*; 16748: 4 *A. zweifeli*; 16749: 7 *Physalopteroides milnensis*, 2 *Abbreviata* sp. (larvae), 6 *A. zweifeli*, 20 *M. crombiei*, 8 *B. bakeri*; 16750: 10 *G. novaeguineanaensis*, 3 *P. maplestoni*, 1 *S. spheonomorphicola*; 16751: 1 *M. crombiei*, 4 *P. maplestoni*, 6 *A. zweifeli*; 16752: 2 *B. bakeri*, 14 *P. maplestoni*, 7 *Mesocoelium breviaecum*; 16753: 6 *G. novaeguineanaensis*, 5 *P. maplestoni*, 2 *M. crombiei*; 16754: 11 *A. zweifeli*; 16755: 1 *P. maplestoni*, 11 *A. zweifeli*; 16756: 15 Rictulariidae gen. sp. (larvae), 1 *S. spheonomorphicola*, 2 *A. zweifeli*, 3 *P. maplestoni*; 16757: 2 *P. maplestoni*, 3 *S. spheonomorphicola*; 16758: 2 *G. novaeguineanaensis*, 2 *S. spheonomorphicola*, 9 *A. zweifeli*; 19823: 1 *G. novaeguineanaensis*; 19824: 14 *A. zweifeli*; 19825: 1 *P. maplestoni*; 19826: 1 *G. novaeguineanaensis*, 13 *A. zweifeli*; 19827: 1 *G. novaeguineanaensis*, 7 *Abbreviata* sp. (larvae); 19828: 6 *A. zweifeli*.

New Britain ($n = 18$)

22010: 6 *A. zweifeli*; 22012: 5 *P. maplestoni*, 3 *M. crombiei*, 1 *Abbreviata* sp. (larva); 22013: 3 *G. novaeguineanaensis*, 1 *P. maplestoni*, 2 *Abbreviata* sp. (larvae); 22015: 32 *M. crombiei*, 3 *Abbreviata* sp. (larvae); 22017: 2 *G. novaeguineanaensis*, 3 *P. maplestoni*, 1 Rictulariidae gen. sp. (larva); 22018: 12 *M. crombiei*; 22019: 1 *A. zweifeli*, 2 *P. maplestoni*, 2 *Abbreviata* sp. (larvae). 22020: 2 *A. zweifeli*, 9 *P. maplestoni*, 4 *Abbreviata* sp. (larvae). 22021: 1 *P. maplestoni*, 15 *M. crombiei*, 2 *Abbreviata* sp. (larvae). 22022: 5 *P. maplestoni*, 2 *M. crombiei*; 22023: 3 *P. maplestoni*;

22025: ———; 22026: 1 *Abbreviata* (larva). 22027: 31 *M. crombiei*; 22028: 4 *G. novaeguineanaensis*; 22029: 1 *G. novaeguineanaensis*, 5 *P. maplestoni*, 9 *A. zweifeli*; 22031: 5 *P. maplestoni*, 12 *M. crombiei*, 2 *Abbreviata* sp. (larvae); 22032: 12 *A. zweifeli*, 4 *Abbreviata* sp. (larvae).

Rossel ($n = 20$)

19857: 3 *P. maplestoni*; 19858: 9 *A. zweifeli*; 19859: 3 *P. maplestoni*, 53 *A. zweifeli*, 2 *Abbreviata* sp. (larvae); 19860: 1 *P. milnensis*, 13 *A. zweifeli*, 3 *M. crombiei*; 19861: 3 *M. crombiei*, 17 *A. zweifeli*, 2 *Abbreviata* sp. (larvae); 19862: 7 *C. zugii*, 2 *P. maplestoni*; 19863: 1 *G. novaeguineanaensis*, 3 *P. maplestoni*, 23 *M. crombiei*; 19864: 1 *B. bakeri*, 28 *M. crombiei*, 1 *A. zweifeli*, 7 *P. maplestoni*, 4 *Abbreviata* sp. (larvae); 19865: 2 *P. maplestoni*, 1 *A. zweifeli*, 5 *M. crombiei*; 19866: 1 *Abbreviata* sp. (larva); 19867: 3 *P. maplestoni*, 2 *M. crombiei*, 3 *Abbreviata* sp. (larvae); 19868: 3 *S. spheonomorphicola*, 1 *P. maplestoni*, 1 *A. zweifeli*; 19869: 1 *S. spheonomorphicola*, 2 *P. maplestoni*; 19870: 9 *S. spheonomorphicola*, 7 *A. zweifeli*, 1 *M. crombiei*, 1 *P. maplestoni*; 19871: 4 *S. spheonomorphicola*, 9 *P. maplestoni*, 3 *Abbreviata* sp. (larvae); 19872: 8 *S. spheonomorphicola*, 2 *P. maplestoni*; 19873: 3 *S. spheonomorphicola*, 20 *M. crombiei*;

19874: 1 *M. crombiei*, 1 Rictulariidae (larva); 19875: 7 *S. spheonomorphicola*, 3 *A. zweifeli*; 19880: 9 *A. zweifeli*.

Sudest ($n = 18$)

19830: 1 Rictulariidae gen. sp. (larva); 19831: 4 *P. maplestoni*; 19833: 5 *P. maplestoni*; 19834: 5 *A. zweifeli*, 16 Rictulariidae gen. sp. (larvae); 19836: 6 *A. zweifeli*; 19837: 1 *P. maplestoni*, 4 *Abbreviata* sp. (larvae); 19839: 4 *A. zweifeli*; 19840: 3 *A. zweifeli*; 19841: 6 *S. sphenomorphicola*, 2 *P. maplestoni*; 19842: 1 *P. maplestoni*, 5 *A. zweifeli*; 19844: 4 *A. zweifeli*; 19845: 2 *P. maplestoni*, 1 *Abbreviata* sp. (larva); 19846: 1 *Abbreviata* sp. (larva); 1 *A. zweifeli*; 19847: 5 *P. maplestoni*, 33 Rictulariidae gen. sp. (larvae); 19848: 3 *S. sphenomorphicola*, 9 *P. maplestoni*; 19849: 5 *P. maplestoni*, 5 *A. zweifeli*; 19852: 1 *S. sphenomorphicola*, 1 *Abbreviata* sp. (larva); 19854: 12 *A. zweifeli*.

Gastrointestinal Helminths in *Nactus* spp. (Squamata: Gekkonidae) from Six Papua New Guinean Islands¹

Stephen R. Goldberg,^{2,5} Charles R. Bursey,³ and Fred Kraus⁴

Abstract: A sample of 128 individuals of the slender-toed geckos *Nactus* spp. from six islands of Papua New Guinea (Bougainville, Fergusson, Misima, New Britain, Rossel, Sudest) was examined for gastrointestinal helminths. Found were one species of Digenea, *Mesocoelium brevicum*; one species of Cestoda, *Gekkotaenia novaeguineensis*; one species of Acanthocephala, *Sauracanthorhynchus sphenomorphicola*; and eight species of Nematoda, *Aplectana zweifeli*, *Bakeria bakeri*, *Cosmocerca zugii*, *Meteterakis crombiei*, *Parapharyngodon maplestoni*, *Physalopteroides milnensis*, *Abbreviata* sp. (larvae in cysts), Rictulariidae gen. sp. (larvae in cysts). A total of 1,256 helminths was found. *Aplectana zweifeli* ($n = 447$), *Parapharyngodon maplestoni* ($n = 238$), and *Meteterakis crombiei* ($n = 221$) were the most abundant helminths. Ten new host records are reported for *Nactus* spp. There was a mean of 7.3 ± 3.1 (3–11) helminth species per island. Bougainville Island had the fewest number of helminth species (3) and Misima Island (11) the highest. *Nactus* spp. are parasitized by generalist helminths that also infect other lizard species.

Keywords: Digenea, Cestoda, Acanthocephala, Nematoda, generalists

THE SLENDER-TOED GECKOS *Nactus* spp., are small to medium-sized, forest-floor geckos of the western Pacific islands, northeastern Australia, and the Mascarene Islands (Kraus 2005, Zug and Fisher 2012). Adults of these species vary greatly in size (22–88 mm snout-vent length) and body mass (0.25–12.8 g) (Kraus 2005, unpubl. data). Twelve species of *Nactus* are currently recognized (Uetz et al.

2020), of which five are known to occur in Papua New Guinea: *Nactus acutus* Kraus, 2005; *Nactus kunan* Fisher and Zug, 2012; *Nactus pelagicus* (Girard, 1858); *Nactus sphaerodactylodes* Kraus, 2005; *Nactus vankampeni* (Brongersma, 1933). Additional species of *Nactus* from New Guinea and surrounding islands are being described by Zug (in press). These are the most common and easily collected geckos in New Guinea and surrounding islands, and they form an important component of the forest-floor communities (FK pers. obs.). Previous reports of helminths in *Nactus* spp. are from *Nactus multicarinatus* (Günther, 1872) and *N. pelagicus* from the Republic of Vanuatu (Bursey et al. 2010, Goldberg et al. 2011) much farther to the east. In this paper, we report on gastrointestinal helminths in *Nactus pelagicus* and five undescribed species of *Nactus* from Papua New Guinea.

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METHODS

A sample of 128 geckos, *Nactus* spp., from six islands in Papua New Guinea (Figure 1)

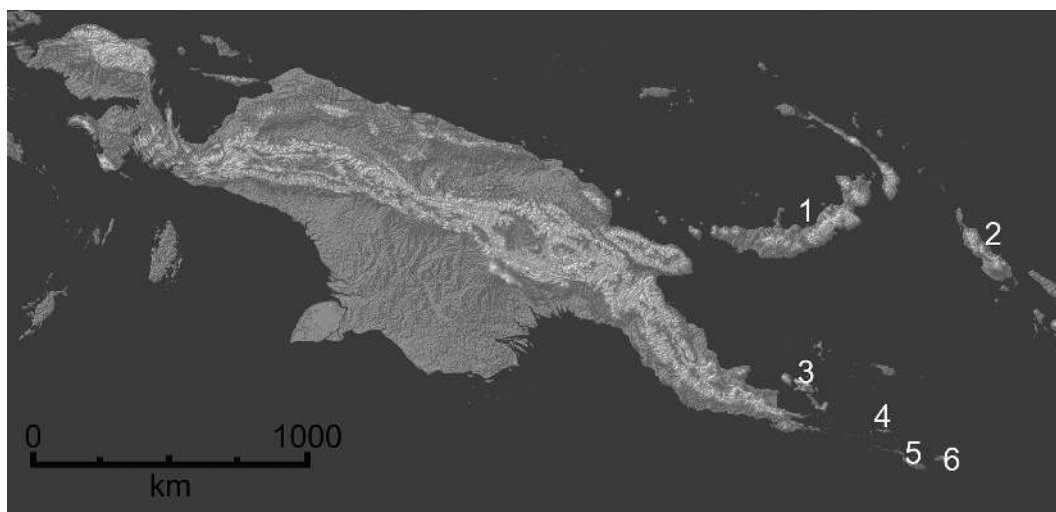


FIGURE 1. Map of Papua New Guinea with island study sites numbered: (1) New Britain; (2) Bougainville; (3) Fergusson; (4) Misima; (5) Sudest; (6) Rossel.

consisting of Bougainville Island, Autonomous region of Bougainville Province (6.3754° S, 155.3807° E), collected 1989 ($n=17$); Fergusson Island, Milne Bay Province (9.5221° S, 150.6750° E), collected 2002 ($n=29$); Misima Island, Milne Bay Province (10.6703° S, 152.7206° E), collected 2003 ($n=26$); New Britain Island, East New Britain Province (5.7466° S, 150.5679° E), collected 2005 ($n=18$); Rossel Island, Milne Bay Province (11.3597° S, 154.1831° E), collected 2004 ($n=20$) and Sudest Island, Milne Bay Province (11.5150° S, 153.4626° E), collected 2004 ($n=18$) was borrowed from the herpetology collection of the Bernice P. Bishop Museum (BPBM), Honolulu, Hawaii, USA (Appendix 1).

Each island sample contained only a single *Nactus* species not shared with any of the other islands, except for Rossel and Sudest, which host two *Nactus* species that occur on both islands. Hence, we examined a total of six species of *Nactus*. Our sample from Bougainville comprises *Nactus pelagicus*; however, the remaining five species are in the process of being described (Zug *in press*). Until the description of these species, we cannot yet distinguish which is involved in our samples from Rossel and Sudest, though the remaining

species will be easily identified because of their endemism (Zug *in press*).

The specimens of *Nactus* spp. were previously fixed in 10% formalin and subsequently stored in 70% ethanol. We opened the body cavity of each specimen by a longitudinal incision and removed the gastrointestinal tract by cutting across the esophagus and rectum. The incision was made using a stainless-steel razor blade, the intestinal wall was pinned with insect pins to remain open, and the contents were examined with a dissecting microscope. Each nematode was removed with jewelers forceps, cleared in lactophenol, examined under a compound microscope, and identified using Anderson *et al.* (2009), Gibbons (2010), or by comparisons with original species descriptions. Acanthocephala, Digenea, and Cestoda were dehydrated in graded alcohol, regressedly stained in hematoxylin, cleared in xylene, and mounted in Canada balsam and studied as whole mounts. Digenea were identified using keys in Dronen *et al.* (2012); Cestoda were identified by comparison to the description in Bursey *et al.* (2005a); Acanthocephala were identified by comparison to the description in Bursey *et al.* (2007). Helminths were deposited in the Harold W. Manter Laboratory

(HWMU), University of Nebraska, Lincoln, USA (Appendix 2). Helminths from each BPBM *Nactus* specimen from each of the six islands from Papua New Guinea are listed in Appendix 3. Definitions of prevalence and mean intensity are in accordance with Bush et al. (1997).

RESULTS

The following helminths were present (Table 1): one species of Digenea, *Mesocoelium breviaecum* Ochi, 1930 (in large intestine); one species of Cestoda, *Gekkotaenia novaeguineensis* Bursey, Goldberg and Kraus, 2005 (small intestine); one species of Acanthocephala, *Sauracanthorhynchus sphenomorphicola* Bursey, Goldberg and Kraus, 2007 (small intestine). Also found were eight species of Nematoda: *Aplectana zweifeli* Moravec and Sey, 1986 (large, small intestines); *Bakeria bakeri* (Moravec and Sey, 1986) (large, small intestines); *Cosmocerca zugi* Bursey, Goldberg and Kraus, 2005 (large intestine); *Meteterakis crombiei* Bursey, Goldberg and Kraus, 2005 (large intestine); *Parapharyngodon maplestoni* Chatterji, 1933 (large intestine); *Physalopteroides milnensis* Bursey, Goldberg and Kraus, 2005 (stomach); *Abbreviata* sp. (larvae in stomach wall cysts); Rictulariidae gen. sp. (larvae in stomach wall cysts).

A total of 1,256 endoparasites were recovered from 112/128 (88%) of *Nactus* spp. (Table 1). There was a mean of 7.3 ± 3.1 (range 3–11) helminth species per island. Ten new host records are reported for *Nactus* spp. (Table 1). *Aplectana zweifeli* ($n = 447$), *P. maplestoni* ($n = 238$), and *M. crombiei* ($n = 221$) were the most abundant helminths. Numbers of other helminths were: *M. breviaecum* ($n = 8$), *G. novaeguineensis* ($n = 33$), *S. sphenomorphicola* ($n = 64$), *B. bakeri* ($n = 22$), *C. zugi* ($n = 21$), *P. milnensis* ($n = 8$), *Abbreviata* sp. ($n = 72$), Rictulariidae gen. sp. ($n = 122$). Bougainville Island had the fewest number of helminth species (3) and Misima Island the most helminth species (11) (Tables 1 and 2).

DISCUSSION

Mesocoelium breviaecum was described by Ochi (1930) from *Ranoidea citropa* (as *Litoria*

citropa Hylidae) from New South Wales, Australia. It is known from a variety of anurans from Japan, Korea, Taiwan, and Vietnam (Prudhoe and Bray 1982). *Gekkotaenia novaeguineensis* was described from *Cyrtodactylus tripartitus* (as *C. louisianensis* Gekkonidae) from Papua New Guinea by Bursey et al. (2005a). *Sauracanthorhynchus sphenomorphicola* was described from *Sphenomorphus granulatus* (Scincidae) by Bursey et al. (2007) from Papua New Guinea; other hosts are listed in Goldberg et al. (2009a, 2010). *Aplectana zweifeli* was described by Moravec and Sey (1986) from *Callulops humicola* (as *Phrynomantis humicola*, Microhylidae) from Papua New Guinea; other Papuan hosts are listed in Goldberg et al. (2009a, b). *Bakeria bakeri* was described from *Callulops stictogaster* (as *Phrynomantis stictogaster*, Microhylidae) by Moravec and Sey (1986) from Papua New Guinea; a host list for *B. bakeri* (as *Oswaldocruzia bakeri*) is in Bursey et al. (2014). *Cosmocerca zugi* was described by Bursey et al. (2005a) from *Cyrtodactylus tripartitus* (as *C. louisianensis*, Gekkonidae) from Papua New Guinea; host lists for *C. zugi* are in Bursey et al. (2014, 2015). *Meteterakis crombiei* was described by Bursey et al. (2005b) from *Sphenomorphus jobiensis* (Scincidae) from Papua New Guinea; host lists for *M. crombiei* are in Bursey et al. (2014, 2015). *Parapharyngodon maplestoni* was described by Chatterji (1933) from *Calotes versicolor* (Agamidae) from Myanmar; host lists for *P. maplestoni* are in Bursey et al. (2014, 2015). *Physalopteroides milnensis* was described from *Sphenomorphus jobiensis* (Scincidae) from Papua New Guinea by Bursey et al. (2005b); hosts for *P. milnensis* are in Goldberg et al. (2008, 2009a, 2010).

Abbreviata sp. and Rictulariidae gen. sp. are both larval helminths not capable of completing their life cycles in lizards. Larvae of *Abbreviata* sp. are common in Australian reptiles (Jones 1995) and are widespread in Papua New Guinea. Lists of hosts for larvae of *Abbreviata* sp. from Papua New Guinea are in Bursey et al. (2014, 2015). Larvae in cysts of Rictulariidae gen. sp. are common in lizards of Papua New Guinea (see Bursey et al. 2014). Infected lizards with *Abbreviata* sp. presumably act as transport hosts when they are eaten

TABLE 1
Number of Helminths (*n*), Prevalence (*P*) in Percent, Mean Intensity ± SD (MI), and Range (*R*) for *Nectus* spp. from Six Islands of Papua New Guinea

Island	Bougainville (<i>n</i> = 17)			Fergusson (<i>n</i> = 29)			Misima (<i>n</i> = 26)		
Helminth	<i>n</i>	<i>P</i>	MI ± SD	<i>R</i>	<i>n</i>	<i>P</i>	MI ± SD	<i>R</i>	<i>R</i>
Digenea									
* <i>Mesocoelium brevicatum</i>					1	3%	1.0		7.0
Cestoda									
* <i>Gekkotaenia novaeguineensis</i>									1–10
Acanthocephala									
* <i>Sauracanthorhynchus sphenomorphicola</i>					11	17%	2.2 ± 1.8	1–5	1–3
Nematoda									
* <i>Aplectana zweifeli</i>	9	29%	2.0 ± 1.0	1–3	131	48%	9.3 ± 11.7	1–45	118
* <i>Bakeria bakeri</i>					11	24%	1.6 ± 1.1	1–4	10
* <i>Cosmocerca zugii</i>	1	6%	1.0		12	21%	2.0 ± 2.4	1–7	1
* <i>Metetraxus crombiei</i>									2–20
* <i>Parapharyngodon maplestoni</i>					62	52%	4.1 ± 3.5	1–13	64
* <i>Physalopteroides milnensis</i>									1–14
* <i>Abbreviata</i> sp. (in cyst)					13	14%	3.3 ± 2.9	1–7	7
* <i>Rictulariidae</i> gen. sp. (in cyst)	9	6%	9.0		24	7%	12.0 ± 7.1	7–17	16
Summary <i>n</i> , <i>P</i>			19, 24%				265, 97%		37
									318, 96%
Island	New Britain (<i>n</i> = 18)			Rossel (<i>n</i> = 20)			Sudest (<i>n</i> = 18)		
Helminth	<i>n</i>	<i>P</i>	MI ± SD	<i>R</i>	<i>n</i>	<i>P</i>	MI ± SD	<i>R</i>	<i>R</i>
Digenea									
* <i>Mesocoelium brevicatum</i>									
Cestoda									
* <i>Gekkotaenia novaeguineensis</i>	10	22%	2.5 ± 1.3	1–4	1	5%	1.0		
Acanthocephala									
* <i>Sauracanthorhynchus sphenomorphicola</i>					35	35%	5.0 ± 3.0	1–9	10
Nematoda									
* <i>Aplectana zweifeli</i>	30	28%	6.0 ± 4.6	1–12	114	50%	11.4 ± 15.6	1–53	45
* <i>Bakeria bakeri</i>					1	5%	1.0		
* <i>Cosmocerca zugii</i>					7	5%	7.0		
* <i>Metetraxus crombiei</i>	107	39%	15.3 ± 12.1	2–32	86	45%	9.5 ± 10.8	1–28	
* <i>Parapharyngodon maplestoni</i>	39	56%	3.9 ± 2.4	1–9	38	60%	3.2 ± 2.4	1–9	35
* <i>Physalopteroides milnensis</i>					1	5%	1.0		
* <i>Abbreviata</i> sp. (in cyst)	21	50%	2.3 ± 1.1	1–4	15	25%	2.8 ± 0.8	2–4	7
* <i>Rictulariidae</i> gen. sp. (in cyst)	1	6%		1.0	1	5%		1.0	50
Summary <i>n</i> , <i>P</i>			208, 95%				299, 100%		147, 100%

* = new host record.

TABLE 2
 Sizes (km²) of Six Islands from Papua New Guinea
 (taken from www.google.com) and Number of Helminth
 Species/Island

Island	Province	Area (km ²)	Number of Helminth Species
New Britain	East New Britain	36,520	5
Bougainville	Autonomous Region of Bougainville	9,300	3
Fergusson	Milne Bay	1,437	8
Sudest	Milne Bay	830	5
Rossel	Milne Bay	293	10
Misima	Milne Bay	215	11

by larger lizards (King and Jones 2016). Members of the Rictulariidae normally parasitize the alimentary tract of mammals and use insects as intermediate hosts; lizards are paratenic (transport) hosts (Anderson 2000).

Most of the helminth species we recovered are known only from Papua New Guinea including: *A. zweifeli*, *B. bakeri*, *C. zugi*, *G. novaeguineensis*, *M. crombiei*, *P. milnensis*, *S. sphenomorphicola*. In contrast, *P. maplestoni*, is widespread in both Asia and the Pacific region and was previously found in the congeners *N. multicarinatus* and *N. pelagicus* from the Republic of Vanuatu (Goldberg et al. 2011). *Mesocoelium brevicacaecum* is widely distributed in the Orient (Prudhoe and Bray 1982). Because the samples we examined were collected in different years, we are unable to make meaningful associations on the occurrence of helminths and correlations with yearly ecological events or environmental phenomena.

None of the above helminths is unique to a single lizard species. Each infects other hosts indicating they are generalist helminths. It thus appears that the occurrence of a particular helminth in a lizard species is the result of chance, reflecting opportunistic feeding habits and the availability of food of the appropriate size (heteroxenous species) or appropriate ecological conditions supporting egg or larval survival (monoxenous species) rather than phylogenetic affinities. As

additional lizards from New Guinea are examined for parasites, we expect the helminth lists for species of *Nactus* will increase.

The helminth community of *Nactus pelagicus* on Bougainville Island is depauperate when compared to the other islands in our study (Tables 1 and 2). We hypothesize that this low helminth diversity, low number of infected individuals low numbers of helminths reported from Bougainville Island (Table 1) are due to attenuation of species numbers due to sequential founder effects in the few hosts that colonized a series of islands in a stepwise fashion to reach Bougainville. This is supported by the fact that *N. multicarinatus* and *N. pelagicus* from Vanuatu, farther east in the Pacific, also had low helminth species numbers: 6 species and 5 species, respectively (Goldberg et al. 2011). In contrast, the other islands in our study were formerly connected to New Guinea (Fergusson, 8 helminth species; Misima, 11 helminth species; Rossel 10 helminth species, Sudest; 5 helminth species) or lie closer to New Guinea and would have required fewer steps to reach (New Britain, 6 helminth species). There seems no obvious relationship between island size (Table 2) and helminth diversity, as has been reported for other lizards (Dobson et al. 1992, Roca 1996).

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APPENDIX 1

Nactus Specimens from Papua New Guinea Islands Examined from the Herpetology Collection of the Bishop Museum (BPBM), Honolulu, Hawaii, USA

Bougainville Island: BPBM 16984–17000. **Fergusson Island:** BPBM 15854–15860, 15862–15870, 15872–15884. **Misima Island:** BPBM 16739–16758, 19823–19828. **New Britain Island:** BPBM 22010, 22012, 22013, 22015, 22017–22023, 22025–22029, 22031, 22032. **Rossel Island:** BPBM 19857–19875, 19880. **Sudest Island:** BPBM 19830, 19831, 19833, 19834, 19836, 19837, 19839–19842, 19844–19849, 19852, 19854.

APPENDIX 2

Harold W. Manter Parasite Collection (HWML), University of Nebraska, Lincoln, USA) Accession Numbers for Helminths from *Nactus* sp. Collected (by island) in Papua New Guinea Examined from the Herpetology Collection of the Bishop Museum (BPBM), Honolulu, Hawaii, USA

Bougainville: *Aplectana zweifeli* (HWML 111607); *Cosmocerca zugii* (HWML 111608); Rictulariidae gen. sp. (larva) (HWML 111609).

Fergusson: *Sauracanthoborhynchus spheonomorphicola* (HWML 111610); *A. zweifeli* (HWML 111611); *Bakeria bakeri* (HWML 111612); *C. zugii* (HWML 111613); *Parapharyngodon maplestoni* (HWML 111614); *Abbreviata* sp. (larva) (HWML 111615); Rictulariidae gen. sp. (larva) (HWML 111616).

Misima: *Mesocoelium breviaecum* (HWML 111617); *Gekkotaenia novaeguineensis* (HWML 111618); *S. spheanomorphicola* (HWML 111619); *A. zweifeli* (HWML 111620); *B. bakeri* (HWML 111621); *C. zugii* (HWML 111622); *Meteterakis crombiei* (HWML 111623); *P. maplestoni* (HWML 111624); *Physalopteroides milnensis* (HWML 111625); *Abbreviata* sp. (larva) (HWML 111626); Rictulariidae gen. sp. (larva) (HWML 111627).

New Britain: *G. novaeguineensis* (HWML 111628); *A. zweifeli* (HWML 111629); *M. crombiei* (HWML 111630); *P. maplestoni* (HWML 111631); *Abbreviata* sp. (larva) (HWML 111632); Rictulariidae gen. sp. (larva) (HWML 111633).

Rossel: *G. novaeguineensis* (HWML 111634); *S. spheanomorphicola* (HWML 111635); *A. zweifeli* (HWML 111636); *B. bakeri* (HWML 111637); *C. zugii* (HWML 111638); *M. crombiei* (HWML 111639); *P. maplestoni* (HWML 111640); *Abbreviata* sp. (larva) (HWML 111641); Rictulariidae gen. sp. (larva) (HWML 111642).

Sudest: *S. spheanomorphicola* (HWML 111644); *A. zweifeli* (HWML 111645); *P. maplestoni* (HWML 111646); *Abbreviata* sp. (larva) (HWML 111647); Rictulariidae gen. sp. (larva) (HWML 111648).

APPENDIX 3

List of Helminths with BPBM Number for *Nactus* spp. from Six Islands from Papua New Guinea Examined from the Herpetology Collection of the Bishop Museum (BPBM), Honolulu, Hawaii, USA. Numbers with no parasite have — behind them.

Bougainville (*n* = 17)

BPBM number: Helminths

16984: 2 *Aplectana zweifeli*; 16985: —; 16986: —; 16987: —; 16988: —; 16989: —; 16990: 3 *A. zweifeli*; 16991: —; 16992: 9 Rictulariidae gen. sp. (larvae), 3 *A. zweifeli*, 1 *Cosmocerca zugii*; 16993: —; 16994: —; 16995: —; 16996: —; 16997: —; 16998: —; 16999: —; 17000: 1 *A. zweifeli*.

Fergusson (*n* = 29)

15854: —; 15855: 3 *A. zweifeli*, 1 *C. zugii*; 15856: 4 *Abbreviata* sp. (larva), 3 *A. zweifeli*; 15857: 2 *A. zweifeli*; 15858: 1 *Bakeria bakeri*, 6 *A. zweifeli*, 7 *C. zugii*; 15859: 1 *Abbreviata* sp. (larva), 2 *B. bakeri*, 1 *C. zugii*, 5 *A. zweifeli*; 15860: 3 *A. zweifeli*, 1 *C. zugii*; 15862: 7 Rictulariidae gen. sp. (larvae), 3

Parapharyngodon maplestoni; 15863: 17 Rictulariidae gen. sp. (larvae), 13 *P. maplestoni*; 15864: 1 *P. maplestoni*; 15865: 8 *A. zweifeli*; 15866: 3 *P. maplestoni*; 15867: 4 *P. maplestoni*; 15868: 4 *P. maplestoni*; 15869: 1 *P. maplestoni*, 1 *Mesocoelium breviaecum*; 15870: 1 *P. maplestoni*; 15872: 1 *A. zweifeli*, 1 *Sauracanthobryncus spheonomorphicola*; 15873: 1 *C. zugii*, 7 *A. zweifeli*; 15874: 1 *S. spheonomorphicola*, 1 *C. zugii*, 17 *A. zweifeli*; 15875: 1 *B. bakeri*, 1 *C. zugii*, 4 *P. maplestoni*, 4 *A. zweifeli*; 15876: 1 *P. maplestoni*, 21 *A. zweifeli*; 15877: 4 *B. bakeri*, 6 *A. zweifeli*; 15878: 1 *S. spheonomorphicola*, 1 *B. bakeri*, 45 *A. zweifeli*; 15879: 8 *Abbreviata* sp. (larva), 5 *S. spheonomorphicola*; 15880: 1 *Abbreviata* sp. (larva), 11 *P. maplestoni*; 15881: 5 *P. maplestoni*, 1 *B. bakeri*; 15882: 4 *P. maplestoni*; 15883: 3 *S. spheonomorphicola*, 3 *P. maplestoni*; 15884: 4 *P. maplestoni*, 1 *B. bakeri*.

Misima (*n* = 26)

16739: ———; 16740: 1 *P. maplestoni*, 10 *A. zweifeli*; 16741: 5 *P. maplestoni*; 16742: 1 *Gekkotaenia novaeguineanaensis*, 8 *P. maplestoni*, 6 *A. zweifeli*; 16743: 1 *S. spheonomorphicola*, 4 *P. maplestoni*, 1 *A. zweifeli*; 16744: 1 *Abbreviata* sp. (larva), 8 *P. maplestoni*; 16745: 22 Rictulariidae gen. sp. (larvae), 8 *A. zweifeli*, 2 *P. maplestoni*; 16746: 3 *P. maplestoni*, 2 *A. zweifeli*; 16747: 6 *Abbreviata* sp. (larva), 1 *C. zugii*, 9 *A. zweifeli*, 5 *Meterakis crombiei*; 16748: 4 *A. zweifeli*; 16749: 7 *Physalopteroides milnensis*, 2 *Abbreviata* sp. (larvae), 6 *A. zweifeli*, 20 *M. crombiei*, 8 *B. bakeri*; 16750: 10 *G. novaeguineanaensis*, 3 *P. maplestoni*, 1 *S. spheonomorphicola*; 16751: 1 *M. crombiei*, 4 *P. maplestoni*, 6 *A. zweifeli*; 16752: 2 *B. bakeri*, 14 *P. maplestoni*, 7 *Mesocoelium breviaecum*; 16753: 6 *G. novaeguineanaensis*, 5 *P. maplestoni*, 2 *M. crombiei*; 16754: 11 *A. zweifeli*; 16755: 1 *P. maplestoni*, 11 *A. zweifeli*; 16756: 15 Rictulariidae gen. sp. (larvae), 1 *S. spheonomorphicola*, 2 *A. zweifeli*, 3 *P. maplestoni*; 16757: 2 *P. maplestoni*, 3 *S. spheonomorphicola*; 16758: 2 *G. novaeguineanaensis*, 2 *S. spheonomorphicola*, 9 *A. zweifeli*; 19823: 1 *G. novaeguineanaensis*; 19824: 14 *A. zweifeli*; 19825: 1 *P. maplestoni*; 19826: 1 *G. novaeguineanaensis*, 13 *A. zweifeli*; 19827: 1 *G. novaeguineanaensis*, 7 *Abbreviata* sp. (larvae); 19828: 6 *A. zweifeli*.

New Britain (*n* = 18)

22010: 6 *A. zweifeli*; 22012: 5 *P. maplestoni*, 3 *M. crombiei*, 1 *Abbreviata* sp. (larva); 22013: 3 *G. novaeguineanaensis*, 1 *P. maplestoni*, 2 *Abbreviata* sp. (larvae); 22015: 32 *M. crombiei*, 3 *Abbreviata* sp. (larvae); 22017: 2 *G. novaeguineanaensis*, 3 *P. maplestoni*, 1 Rictulariidae gen. sp. (larva); 22018: 12 *M. crombiei*; 22019: 1 *A. zweifeli*, 2 *P. maplestoni*, 2 *Abbreviata* sp. (larvae). 22020: 2 *A. zweifeli*, 9 *P. maplestoni*, 4 *Abbreviata* sp. (larvae). 22021: 1 *P. maplestoni*, 15 *M. crombiei*, 2 *Abbreviata* sp. (larvae). 22022: 5 *P. maplestoni*, 2 *M. crombiei*; 22023: 3 *P. maplestoni*;

22025: ———; 22026: 1 *Abbreviata* (larva). 22027: 31 *M. crombiei*; 22028: 4 *G. novaeguineanaensis*; 22029: 1 *G. novaeguineanaensis*, 5 *P. maplestoni*, 9 *A. zweifeli*; 22031: 5 *P. maplestoni*, 12 *M. crombiei*, 2 *Abbreviata* sp. (larvae); 22032: 12 *A. zweifeli*, 4 *Abbreviata* sp. (larvae).

Rossel (*n* = 20)

19857: 3 *P. maplestoni*; 19858: 9 *A. zweifeli*; 19859: 3 *P. maplestoni*, 53 *A. zweifeli*, 2 *Abbreviata* sp. (larvae); 19860: 1 *P. milnensis*, 13 *A. zweifeli*, 3 *M. crombiei*; 19861: 3 *M. crombiei*, 17 *A. zweifeli*, 2 *Abbreviata* sp. (larvae); 19862: 7 *C. zugii*, 2 *P. maplestoni*; 19863: 1 *G. novaeguineanaensis*, 3 *P. maplestoni*, 23 *M. crombiei*; 19864: 1 *B. bakeri*, 28 *M. crombiei*, 1 *A. zweifeli*, 7 *P. maplestoni*, 4 *Abbreviata* sp. (larvae); 19865: 2 *P. maplestoni*, 1 *A. zweifeli*, 5 *M. crombiei*; 19866: 1 *Abbreviata* sp. (larva); 19867: 3 *P. maplestoni*, 2 *M. crombiei*, 3 *Abbreviata* sp. (larvae); 19868: 3 *S. spheonomorphicola*, 1 *P. maplestoni*, 1 *A. zweifeli*; 19869: 1 *S. spheonomorphicola*, 2 *P. maplestoni*; 19870: 9 *S. spheonomorphicola*, 7 *A. zweifeli*, 1 *M. crombiei*, 1 *P. maplestoni*; 19871: 4 *S. spheonomorphicola*, 9 *P. maplestoni*, 3 *Abbreviata* sp. (larvae); 19872: 8 *S. spheonomorphicola*, 2 *P. maplestoni*; 19873: 3 *S. spheonomorphicola*, 20 *M. crombiei*;

19874: 1 *M. crombiei*, 1 Rictulariidae (larva); 19875: 7 *S. spheonomorphicola*, 3 *A. zweifeli*; 19880: 9 *A. zweifeli*.

Sudest ($n = 18$)

19830: 1 Rictulariidae gen. sp. (larva); 19831: 4 *P. maplestoni*; 19833: 5 *P. maplestoni*; 19834: 5 *A. zweifeli*, 16 Rictulariidae gen. sp. (larvae); 19836: 6 *A. zweifeli*; 19837: 1 *P. maplestoni*, 4 *Abbreviata* sp. (larvae); 19839: 4 *A. zweifeli*; 19840: 3 *A. zweifeli*; 19841: 6 *S. sphenomorphicola*, 2 *P. maplestoni*; 19842: 1 *P. maplestoni*, 5 *A. zweifeli*; 19844: 4 *A. zweifeli*; 19845: 2 *P. maplestoni*, 1 *Abbreviata* sp. (larva); 19846: 1 *Abbreviata* sp. (larva); 1 *A. zweifeli*; 19847: 5 *P. maplestoni*, 33 Rictulariidae gen. sp. (larvae); 19848: 3 *S. sphenomorphicola*, 9 *P. maplestoni*; 19849: 5 *P. maplestoni*, 5 *A. zweifeli*; 19852: 1 *S. sphenomorphicola*, 1 *Abbreviata* sp. (larva); 19854: 12 *A. zweifeli*.