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A preliminary assessment of the *Nactus pelagicus* species group (Squamata: Gekkonidae) in New Guinea and a new species from the Admiralty Islands

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Abstract

The Slender-toed Geckos (*Nactus*) currently have four recognized species in New Guinea, and these species divide into two sister clades: a *pelagicus* clade and a *vankampeni* clade (Heinicke *et al.* 2010). The latter contains three dwarf species. The former consists of five bisexual populations, of which numerous New Guinea populations are uncharacterized nomenclaturally and lumped under the epithet '*pelagicus*.' This report and description of a new species of the *pelagicus* group from Manus Island in the Admiralty Islands encourages us to offer a preliminary assessment of morphology and diversity in New Guinea '*pelagicus*' populations.

Key words: *Nactus pelagicus* group, New Guinea, Admiralty Islands, morphology, geographic variation, new species

Introduction

The Slender-toed Geckos, *Nactus*, are small to modest-sized, forest-floor geckos of the west Pacific islands and northeastern Australia. A muted color pattern of dark shades of brown hides them from visual predators and similarly has given them a low profile with field naturalists and museum taxonomists. For much of the 20th century, two species were recognized: *Nactus vankampeni*, a dwarf morph from the northern coast of Papua New Guinea; and *Nactus pelagicus*, a modest-sized morph from New Guinea and adjacent islands westward into Oceania. Actually, both resided in the genus *Gymnodactylus* or *Cyrtodactylus* for three-quarters of the century. Field and genetic studies began to change the concept of *N. pelagicus* as a single species when Schwaner (1980) discovered that all members of his large sample from Samoa were females. Subsequently, Moritz's (1987) genetic study (karyotypes and allozymes) of numerous Southwest Pacific populations confirmed the parthenogenetic nature of the Oceania populations and uncovered a greater diversity among the bisexual populations than anticipated. He defined the geographical distribution of the parthenogenetic populations and demonstrated that the genetic differences among the bisexual populations were large and each genotype likely represented a different species.

In 1995, Zug and Moon assessed the morphology of the Solomons, Vanuatu, and oceanic populations. They recognized *Nactus pelagicus* as the asexual species for the populations in southern Vanuatu and elsewhere in Oceania, and *N. multicarinatus* for the bisexual species from Vanuatu and the southern Solomon Islands. Also in 1995, Donnellan and Moritz presented additional genetic evidence of the molecular diversification within this group. They determined that their Australian, New Guinea, and Oceania samples minimally contained four (likely six) bisexual species that were genetically divergent from each other (see final section "Emerging relationships" for the significance of their discoveries) and, in part, led Zug (1998) to examine Australian populations and resurrect *N. cheverti* and *N. eboracensis*. One of the bisexual species included in the Donnellan's and Moritz's (1995) analysis was the Vanuatu populations that Zug and Moon had designated as *N. multicarinatus*. *N. multicarinatus* was a member of their Group IV, whose populations occurred from the central-north coast of Papua New Guinea through

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the Bismarcks to Efate, Vanuatu. Zug and Moon (1995) speculated that most Solomon Islands' populations were *N. multicarinatus*, but they specifically excluded populations of eastern Papua New Guinea owing to differences in morphology uncovered in an earlier preliminary analysis. Heinicke *et al*. (2010) demonstrated that the southern Solomon Islands' *N. multicarinatus* are closely related to the Vanuatuan ones, confirming Zug and Moon's (1995) conclusion.

The nomenclatural status of New Guinean populations remains unaddressed, but not unstudied. One of us (GRZ) has continued to gather morphological data on populations of the *Nactus pelagicus* group throughout New Guinea. This data gathering has revealed a much higher level of differentiation than reported heretofore. As noted above, a greater species diversity had been revealed previously by molecular studies (Donnellan & Moritz 1995; Heinicke *et al*. 2010) of *Nactus* populations, although the goals of these studies have been focused on the identification of lineages.

While recent studies demonstrate numerous species, early exploration of New Guinean reptile fauna recognized few species (Table 1). Only two names, *Gymnodactylus arfakianus* Meyer and *Heteronota fasciata* Macleay, apply to mainland New Guinea populations. The first name is available; however, the type has been lost and the type locality is just New Guinea. The use of this name will require the designation of a neotype and a redescription of the taxon. *Heteronota fasciata* was proposed unwittingly as a homonym and was replaced by *G. heteronotus* (Boulenger 1895). Because the named population has a precise location and the holotype is extant, the name can be associated with one of several south coast New Guinea species. The assignment and re-characterization of this taxon will occur in a subsequent publication. The *Nactus pelagicus* group population on Great Kei was recognized as distinct by Kopstein (1926); he described it as a subspecies *Gymnodactylus pelagicus undulatus*. Thus, only three names are potentially available for New Guinean populations of this wide-ranging gecko, which upon close examination shows the high level of diversity seen in other New Guinea reptiles. Its generally dull coloration, especially after preservation, attracted little attention to these geckos by early European naturalists and a minimal nomenclatural history.

TABLE 1. Names proposed for New Guinea area populations of the *Nactus pelagicus* species group.

DATE	NAME	AUTHOR	TYPE LOCALITY
1874	*Gymnodactylus* (*Heteronota*) *arfakianus*	Meyer	"Neu-Guinea"
1878	*Heteronota fasciata*	Macleay	"Hall Sound"
1878	*Heteronota eboracensis*[1]	Macleay	"Cape York"
1885	*Gymnodactylus heteronotus*[2]	Boulenger	
1926	*Gymnodactylus pelagicus undulatus*	Kopstein	"Elat, Gross-Kei"

[1] *Nactus eboracensis* is an Australian species and presently unknown in New Guinea (Zug 1998); however, it occurs in many of the islands of the Torres Straits and thus its presence in southwestern Papua New Guinea and/or southeastern Papua Indonesia is possible. No vouchers of *Nactus* are available for the latter area. Actually, there are very few museum specimens of *Nactus* from western half of New Guinea, i.e., Papua-Indonesia.

[2] Macleay's *H. fasciata* was a homonym. Boulenger (1885) offered the replacement name *G. heteronotus*.

But not all *Nactus* are dull. The Black Mountain Slender-toed Gecko, *Nactus galgajuga*, is a striking black and white banded gecko. The USGS-PNGNM survey of Manus Island discovered a forest *Nactus* that is even more striking than *N. galgajuga*. This gecko is black and yellow banded and strikingly different from the other Manus Island *Nactus*, which appears to be unisexual and likely represents a recent introduction of *N. pelagicus* from the Pacific. Both species are examined in more detail below. First, however, we offer a brief review of morphological traits that serve to differentiate the currently recognized and potential new *Nactus* species of the Pacific area.

Materials and methods

The morphological characters used in this study are the same as those used in the study of geographic variation of Australian *Nactus* (Zug 1998). Those characters are listed below. The character set contains 12 mensural and 18 scalation (meristic) characters, although not all characters are reported herein. All mensural characters are straightline measurements of body segments to the nearest 0.1 mm with dial calipers. Scalation features of head, body and limbs recorded from right side on bilaterally paired features. Sex and reproductive state (maturity) determined by dissection and examination of the gonads. Mature females possess vitellogenic follicles >1.5 mm, oviducal eggs, or stretched but empty oviducts; mature males have enlarged testes and epididymides. Determination of maturity for female is more reliable for maturing lizards owing to the discreteness of virginal versus nonvirginal oviducts in females compared to the recognition of "enlarged" testes in males. Data for the examined specimens are below in the Appendix. All statistical analyses were performed with SYSTAT 11. Sexual dimorphism among adults was tested by Student's t tests ($p<0.05$).

The following list provides character names and their abbreviations. Definition details are available in Zug (1998), although the character name is often sufficient to define the characters owing to their common usage in lizard systematic studies.

Measurements: Eye diameter (EyeD); Head height (HeadH); Head length (HeadL); Interorbital width (Interorb); Jaw width (JawW); Naris-eye length (NarEye); Neck length (NeckL); Snout width (SnW); Snout-forelimb length (SnForel); Snout-vent length (SVL); Tail length (TailL); Trunk length (TrunkL).

Scalation: Cloacal spurs (CloacS); Cloacal spur's tip (CSTip); Rows of dorsal tubercles (DorsTub); Femoral pores (FemPor); Forefoot lamellae (ForefLm); Hindfoot lamella (HindfLm); Infralabial scales (Inflab); Palm scales (Palm); Postmental-infralabial contact (PmLab); Femoral and precloacal pores contact (PoreC); Postmental scale size (Postm); Precloacal pores (PreclPor); Subcaudal scales (Subcaud); Supralabial scales (Suplab); Tubercles in a parasagittal tubercle row (TubRow); Tubercle rows over hips (TubHip); Tubercle distribution on hindlimb (TubHindl); Tubercle density on thigh (TubDens).

For the genetic analyses, we downloaded all sequences used by Heinicke *et al.* (2010) from GenBank (see their Table 1; Figure 1) for the *Nactus* ingroup and all of the *Heteronotia* and *Dixonius* as outgroups). Their dataset consists of multiple mitochondrial and nuclear genes, although we only analyze a subset of the data used in their study (mtDNA: 740bp; RAG-1: 279bp; PDC: 360bp; primer sets listed below).

Additional sequences were generated to assess the relationship of *Nactus kunan* **sp. nov.** within the phylogeny and to further assess the *pelagicus-multicarinatus* clade. We used Qiagen DNeasy blood and tissue kit (Qiagen, Valencia, California, USA) to isolate genomic DNA from ethanol preserved or frozen tissues collected by RNF (Table 4) according to the manufacturers' directions. We used three previously published primer sets from Jackman et al. (2008) to PCR amplify and sequence each of the three loci utilized in this study. The mitochondrial loci were sequenced using L4437b (Macey *et al*. 1997) and H5934a (Arevalo *et al.* 1994), primers R13 and R18 for RAG-1 (Groth & Barrowclough 1999), and primers PhoF2 and PhoR1 for the Phosducin (PDC) locus (Bauer *et al.* 2007). All three loci were amplified using a thermal profile of 95°C for 2 min (initial denaturation), followed by 35 cycles of 95°C for 30 s, 54°C for 45 s, and 72°C for 1 min, followed by an 8 min extension at 72°C. PCR products were sequenced commercially by GENEWIZ (South Plainfield, NJ, USA). Sequences were aligned by eye and neighbor joining trees that also included sequences analyzed by Heinicke *et al.* (2010) were constructed initially using TOPALi version 2.5. The mitochondrial loci were analyzed separately from the nuclear loci which were combined in a single data file.

Bayesian methods were utilized for phylogenetic analyses, with separate analyses conducted for the mitochondrial loci and the combined nuclear genes. Akaike Information Criteria (AIC) scores were generated using jModeltest 0.1 (Posada 2008) to determine the best fitting evolutionary models. The selected models were as follows: GTR+I+Γ for ND2; HKY+G for RAG-1; and SYM+G for PDC. The Bayesian analyses were run in BEAST 1.6.1, for 30,000,000 generations, with the first 10% discarded as burn-in for all analysis. Posterior probabilities were used to determine branch support. The dataset utilized to generate the phylograms (Figure 2, 3) included a total of 1379 bp (740 bp mtDNA, 279 bp RAG-1, 360 bp PDC). For the mitochondrial dataset, 454 sites were variable and 391 were parsimony-informative. For the combined nuclear dataset, 144 sites were variable and 111 were parsimony-informative.

Morphological characters of *Nactus pelagicus* species group members

When Zug and Moon (1995) initiated their examination of variation of the *pelagicus* group, they assembled a list of characters used in previous publications on this group and added other traits that might discriminate among different populations. This initial set of characters was modified subsequently with additions and deletions in a systematic study of Australian population (Zug 1998). Rösler *et al.* (2005) examined additional characters. The following discussion is a brief assessment of some of these characters. The standard character set used in Zug's previous studies is detailed above. We also examine morphological traits that other researchers, e.g., Rösler *et al.* (2005) and Kraus (2005), identified as diagnostic among populations of *Nactus*.

Adult size, either as average SVL of mature individuals or as minimum SVL at maturation, discriminates between the two *Nactus* clades (*pelagicus* [38–86 mm SVL] and *vankampeni* [20–38 mm] groups) and populations within each clade; for example, *N. eboracensis* adults range 38–58 mm SVL and *N. multicarinatus* 43–63 mm. All other mensural traits correlate strongly with SVL, showing a similar pattern of size-relatedness within and among taxa. Proportions and multivariate statistics offer a potential of discovering diagnostic features among the other mensural traits, but an in-depth analysis of mensural traits has not been done. Zug and Moon (1995) tentatively identified HeadH and EyeD as potential discriminators.

Features of scalation are the major discriminators among populations/species of *Nactus.* The shape and size of the rostral scale potentially differs among populations, but as yet no one has proposed a standardized measurement. Similarly, the rostral is variably depressed posteromedially and typically bears a midline cleft; neither of these aspects has been characterized for a quantitative comparison among populations. There are differences in the size and shape of the supranasals and whether they abut on the dorsal midline. Rösler *et al*. (2005) noted the latter aspect by their number of internasal scales character. When the supranasals are large and rectangular, they contact broadly on the dorsal midline and no internasal scales exist. Some *Nactus* populations have reduced supranasals and the smaller supranasals become semilunate in shape allowing the dorsal granular head scales to extend forward to contact the posterior edge of the rostral. Rösler et al. did not define how they counted these "internasal" scales; we recommend counting only the number of granular scales contacting the rostral scale.

The nasal scale is a large scale bordered on three sides by the supranasals, rostral, and first infralabial. It contains a large naris and a broad shelf extending posterior from the naris. F. Kraus (*in litt.* March 2009) noted that lowland and montane populations of Milne Bay area *Nactus* differed by the number of granular scales contacting this posterior shelf. This trait potentially distinguishes other *Nactus* populations and has another feature, the relative size of the dorsalmost granular scale to the more ventral ones, although it has not been quantified to permit estimates of variation within and between populations. The size of the supra- and infralabial scales (Suplab, Inflab) is portrayed by the number of entire scales lying in front of the anterior border of the eye; other researchers have counted from the middle of the eye or the beginning of the labial rictus. No matter how defined, the exact endpoint requires a recorder's interpretation, hence the potential of increased variation.

The size and shape of the mental scale, size and shape of the postmental scales (Postm), and first infralabial-postmental contact (PmLab) are a set of related features of the chin. As yet, their changing states have not been integrated, in part owing to the difficulty of quantifying the various states of the three characters. Rösler *et al.* (2005) quantified mental size by two states (wider than long, as wide as long); this quantification ignores the changing shape of the mental, which ranges from near triangular to distinctly pentagonal, and is also too subjective without actually measuring width and length. We cannot offer a standardization and provide only a descriptor of shape. Zug and Moon (1995: fig. 5) noted the broad range of sizes of the postmentals from absent (indistinguishable from granular chin scales) to large; they offer a quantification of size by equating the area of the right postmental with number of granular chin scales occupying an equivalent area (Postm). Rösler *et al*. (2005) proposed a different quantification, relative size of postmental compared to the first supralabial expressed as a percent. As the postmental decreases in size, its position in the mental-infralabial notch sometimes shifts downward on the mental edge. When this occurs, chin scales intrude between the postmental and the first infralabial. The number of transverse rows of intruding chin scales (PmLab) characterizes this shift as well as the reduction in postmental size.

Nactus is usually characterized by presence of rows of enlarged, various carinate tubercles on the dorsum of the trunk. Most researchers report this character by the number of longitudinal rows (DorsTub). This quantification appears adequate although the ventralmost rows on each side of the trunk are commonly incomplete and may or may not be counted thereby increasing the variation of this character and potentially reducing its diagnostic aspect. Another feature of the tubercle rows is the number of tubercles in one of the longitudinal rows (TubRow). This number reflects the relative separation of tubercles. This separation is also reflected by the number of dorsal granular scales lying between each tubercle in a row; the number of granular scales ranges between one and three, and is fairly consistent within a row and between rows. Separation by a single granular scale yields rows with more tubercles. Other aspects of tubercle rows include number of tubercles between the hindlimbs (TubRow) and number of tubercle rows on the neck.

The nature of the ventral scales on the trunk, when mentioned, is described usually as small and weakly carinate (keeled). Interpopulational variation appears greatest with a unicarinate condition in a few populations as well as smooth ventral scales in others (*N. galgajuga*). Keeled versus smooth scales also occurs for the subcaudal scales (Subcaud). Most members of the *N. pelagicus* group have keeled subcaudals, but keelless subcaudals are characteristic of all Australian *Nactus* and in a few New Guinean populations as well. Male *N. pelagicus* group member typically have a V-shaped row of a dozen or less precloacal pores (PreclPor). The pores may be continuous on the midline or separated by one, occasionally two poreless scales. The presence or absence of a poreless scale occurs within populations, but the level of variation has not been quantified. Femoral pores (FemPor) are commonly absent and typically so in New Guinea populations. When present, their number is low, and they are not continuous (PoreC = 0) with the precloacal pores, typically separated by a five or more scales.

The dorsal surface of fore- and hindlimbs variously bear enlarged carinate tubercles similar to those on the trunk. The upper arm usually lacks tubercles; the lower or forearm bears a few scattered tubercles or is free of tubercles. With or without forearm tubercles is a populational trait, although again not quantified. The presence and absence of tubercles on the hindlimb (TubHindl) has been quantified as three states: tubercles on both upper and lower leg, on lower leg only, and absent on both. The number or density of tubercles varies on both upper and lower limbs and is partially coded by an upper limb character (TubDens) that recognizes three states from few to many (few small granular scales) tubercles on the posterior half of the dorsal surface of the thigh. There are likely more states of tubercle density and distribution but a comparative survey is presently lacking.

The number of lamellae beneath the digits is a common character for distinguishing populations of lizards and is recorded for both the fore- (ForefLm) and hindfoot (HindfLm) of *Nactus*. Kraus (2005) observed that *N. vankampeni* group gecko had four or five scales surrounding the claw in contrast to two or three scales in *N. pelagicus* group geckos. The former character state does not, however, appear to be confined solely to the *vankampeni* group.

The preceding characters and their multiple states provide a wealth of traits for revealing the diversity among the previously assumed dull and nondescript slender-toed geckos of New Guinea. Our on-going investigation of morphological variation suggests that more than a dozen species currently hide beneath the ‘pelagicus’ rubric.

Admiralty Islands *Nactus pelagicus* species group members

Our examination of *Nactus* specimens from the Admiralty Islands identifies two distinct morphotypes. One of them shares characteristics with populations of *Nactus pelagicus* from Oceania. The other morphotype is striking in its color pattern, differing from any other *Nactus* population; this morphotype also possesses a number of differences in scalation and is also genetically very distinctive. It represents a new species.

Nactus kunan sp. nov. Fisher & Zug

(Fig. 1)

Holotype. USNM 576300, adult female from Papua New Guinea, Admiralty Islands, Manus Island, Sohoniliu Village [2.11296S 147.14912E], collected by Robert N. Fisher and villagers from Sohoniliu Village, 26 May 2010.

Paratype. Same collection data as holotype PNGNM 25190 (RNF8981), juvenile female.

Diagnosis. *Nactus kunan* **sp. nov.** is a member of the *Nactus pelagicus* species group and differs from all other members except *N. galgajuga* by a pattern of broad alternating dark (black or dark brown) and light bands on neck, trunk, and tail. It differs from *N. galgajuga* by the golden yellow of its light bands instead of the white bands of *N. galgajuga*. *N. kunan* **sp. nov.** also possesses a unique head pattern among *Nactus* taxa with a sharply contrasting yellow crown and eyelids on a black background.

Description of holotype. An adult female, 56.6 mm SVL, 57 mm tail length (~53 mm regenerated), 23.8 mm TrunkL, 22.5 mm SnForel, 14.8 mm HeadL, 9.9 mm JawW, 6.3 mm HeadH, 3.8 mm EyeD, 5.1 mm NarEye, 4.4 mm Interorb, 2.0 mm SnW. Body proportions, 42% TrunkL/SVL, 40% SnForel, 26% HeadL/SVL, 18% JawW/SVL, 67% JawW/HeadL, 4% EyeD/SVL, 14% EyeD/HeadL, 35% NarEye/HeadL, 30% Interorb/HeadL, 14% SnW/HeadL.

FIGURE 1. *Nactus kunan* **sp. nov.** of Manus Island, Admiralty Islands, Papua New Guinea. A. dorsal aspect of whole body of the holotype USNM 576300; B, dorsal aspect of head of holotype; C, dorsal view of the juvenile and paratype PNGNM 25190 (RNF8981).

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal rectangular rostral scale with a slight middorsal notch, cleft on midline of middorsal half and distinctly depressed on its mid-posterior two-thirds; five large supralabials (left and right, Suplab) and four infralabials (left and right, Inflab) in front of anterior edge of orbit, first supra- and infralabials largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal, and posteriorly four granular loreal scales, dorsalmost one largest. Supranasals moderate sized separated on midline by four granular scales contacting rostral. Scales on outer edge of eyelid slightly enlarged forming low crenate border. Chin with large trapezoidal mental and no postmentals (PostM = 0). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape unto tail; on trunk rows reach ventrolaterally to edge of venter, 17 entire rows (DorsTub), and only to mid-laterally on neck; tubercles in each row usually separated by single granular scale yielding 47 tubercles per row (TUBROW); 8 rows transversely between hindlimbs (TubHip). Few scattered tubercles on dorsal half of forelimb; hindlimb with numerous tubercles (TubHindl = 2), and tubercles abundant fore and aft (TubDens = 1). Base of tail with tubercle rows dorsally, laterally, and slightly overlapping onto ventral surface. Tail nearly totally regenerated and regenerated portion covered with uniform small keeled scales (Subcaud = 0). Pair of cloacal spurs (CloacS) on right, none on left; distal edge truncate (CST = 0). Ventral scales from chin to vent small, granular and unicarinate or tricarinate. Forefoot with narrow digits, their lengths 2≈3≈4>1≈5; 18 lamellae beneath fourth digit (4FingLm), 4 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths 3≈4>5>2>1; 20 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as row of greatly enlarged scales.

TABLE 2. Summary of variation in select mensural characters in adult samples of the *Nactus pelagicus* species group. Mean ± 1 standard deviation, range, and statistically significant dimorphism * (Student's t $p \leqslant 0.05$); sample size in brackets; SVL & HeadL in mm.

TAXON	**SVL**	**TRUNKL/SVL**	**SNFOREL/SVL**	**HEADW/HEADL**	**EYED/HEADL**	**SNW/HEADL**
Nactus pelagicus (Fiji Ids)						
females [27]	58.5±6.61	0.42±0.029	0.41±0.020	0.68±0.047	0.28±0.025	0.15±0.011
	48.0–70.0	0.34–0.46	0.37–0.44	0.59–0.75	0.23–0.33	0.12–0.17
Nactus pelagicus (Admiralty Ids.)						
females [21]	56.6±2.90	0.38±0.032	0.42±0.010	0.70±0.056	0.23±0.032	0.15±0.008
	49.1–61.1	0.32–0.42	0.37–0.46	0.57–0.78	0.17–0.29	0.13–0.17
Nactus kunan **sp. nov.** (Manus Isl.)						
females [1]	56.6	0.42	0.40	0.69	0.26	0.14
Nactus galgajuga (Australia)						
adults [5]	47.5±2.07	0.42±0.039	0.43±0.039	0.66±0.021	0.29±0.024	0.16±0.008
(4 females)	44.3–50.0	0.37–0.49	0.42–0.45	0.62–0.68	0.24–0.31	0.15–0.17
Nactus eboracensis (Australia)						
females [25]	47.9±4.08*	0.42±0.019	0.40±0.019	0.69±0.049*	0.27±0.023	0.15±0.013
	41.1–56.7	0.37–0.46	0.38–0.44	0.63–0.82	0.22–0.30	0.12–0.18
males [34]	45.8±3.70*	0.41±0.028	0.42±0.029	0.67±0.033*	0.27±0.021	0.16±0.014
	37.9±53.5	0.34–0.45	0.34–0.50	0.61–0.75	0.22–0.31	0.12–0.17
Nactus multicarinatus (Vanuatu)						
females [35]	53.7±3.79	0.41±0.030	0.42±0.024	0.70±0.028	0.26±0.030	0.15±0.012
	46.7–59.8	0.37–0.49	0.38–0.47	0.65–0.76	0.22–0.33	0.12–0.18
males [26]	51.8±3.52	0.40±0.020	0.41±0.020	0.70±0.030	0.26±0.032	0.15±0.010
	45.6–58.2	0.37–0.43	0.37–0.44	0.65–0.75	0.22–0.33	0.13–0.18
Nactus sp[1] (Madang Province)						
females [27]	57.5±4.43*	0.41±0.005	0.40±0.020	0.66±0.056	0.13±0.013	0.15±0.016
	47.0–64.3	0.35–0.46	0.37–0.44	0.47–0.73	0.10–0.16	0.09–0.17
males [24]	53.5±3.83*	0.40±0.022	0.41±0.021	0.66±0.048	0.14±0.012	0.15±0.013
	48.2–61.0	0.34–0.44	0.38–0.46	0.56–0.74	0.12–0.16	0.13–0.18

[1] Three *Nactus pelagicus* group morphotypes occur in the coastal lowlands of Madang Province. We selected the most abundant morphotype for comparison with the Admiralty Islands' populations. The selected morphotype displays sexual dimorphism in SVL, TrunkL, SnForel, HeadL, and PmLab.

In life, *N. kunan* is a strikingly bright gecko of alternating yellow and black on the dorsum and sides (Fig. 1A). Dorsal surface of head predominantly yellow from tip of snout to first black transverse bar on nape. Various sized black markings on dorsal surface of head: small, longitudinal one over supranasal suture, small round one on midline in middle of snout, narrow interorbital bar at anterior end of orbit, small, ill-defined marks on crown, and small white scarred area on parietal area (Fig. 1B). Black, irregular edged stripe from nares above ear-opening to groin; dorsally bordered by narrow, clear yellow postocular stripe ending at posterior end of head. Upper and lower lips with alternating bars of black and yellow; yellow ones about half width of black ones and centered on interlabial sutures of both upper and lower lips. Neck and trunk with six black transverse bars at nape, mid neck, three on trunk, and sacral one, clefted by yellow on dorsal midline; neck and trunk bars extending ventrally, nearly to venter. Black bars become bands encircling tail (based on paratypes (Fig. 1C), holotype's tail largely regenerated with only the black band at base); yellow interspaces on trunk about two-thirds width of black on trunk and less than half on tail. Dorsally fore- and hindlimbs also yellow and black, transverse barring better developed on hindlimbs. Venter, including limbs, is dusky brown from chin onto base of tail.

In preservative, yellow color is brownish white; pattern as described above.

Description. A moderate-sized *Nactus* with body proportions of two individuals: 42% TrunkL/SVL, 40% SnForel, 26% HeadL/SVL, 18% JawW/SVL, 67% JawW/HeadL, 4% EyeD/SVL, 14% EyeD/HeadL, 35% NarEye/HeadL, 30% Interorb/HeadL, 14% SnW/HeadL.

The paratype differs little from holotype. It possesses 4 Suplab and 3 Inflab, 16 Dorstub, 45 TubRow, 23 HindfL, and 6 Palm. Both specimens are females and lack preanal and femoral pores. Paratype is reproductively a subadult. The yellow color of the holotype was a muted grayish white in paratype when alive. We tentatively suggest an ontogenetic color shift at maturation and suspect no sexual dimorphic differences in adults.

Distribution. Presently known only from Sohoniliu Village, Manus Island of the Admiralty Archipelago. Papua New Guinea. Probably widespread in the highlands of Manus Island where forest patches remain intact.

Etymology. The specific name comes from the Tokples people's (Nali language) term for bumblebee; this is in reference to the striking bicolor yellow and black banding of holotype (Fig. 1A).

Comparison to other taxa. *Nactus kunan* **sp. nov.** was compared to other *Nactus pelagicus* complex individuals (Tables 2, 3) from Manus and Los Negros Islands in the Admiralty Archipelago, the dominant (most abundant) *N. pelagicus* group member on the adjacent mainland (Madang Province), *N. multicarinatus* from Vanuatu, and two species (*N. eboracensis*, *N. galgajuga*) from Australia. Presently, except for *N. galgajuga* and *N. kunan* **sp. nov.**, all known species, undescribed ones as well, of the *Nactus pelagicus* and *vankampeni* groups have a brown to medium-dark brown ground color with dark brown bars on the dorsum from head to tail. *N. galgajuga* and *N. kunan* **sp. nov.** are transversely banded in dark and light colors. The dark color is black in both taxa; the light color is white in the former and yellow in the latter. *N. kunan* has a robust habitus, perhaps slightly heavier than the average *N. pelagicus* but distinctly heavier than the emaciated habitus of *N. galgajuga*. The slender habitus of *N. galgajuga* give the impression that it has longer limbs than the other *Nactus* species; its limb lengths are the same, although strikingly more slender. Among other differences, *N. galgajuga* has unkeeled scales on the ventral trunk and beneath the tail in contrast to the distinctly keeled scales of *N. kunan* **sp. nov.**

N. kunan **sp. nov.** is larger than any member of the *N. vankampeni* group, and assuming the SVL of the holotype is about average, *N. kunan* **sp. nov.** is the same size as the unisexual *N. pelagicus* and many New Guinea bisexual populations of the *pelagicus* group (Table 2), although distinctly larger than the Australian species (*N. cheverti*, adult females 41–57 mm SVL; *N. eboracensis* adult females 42–57 mm). *N. kunan* **sp. nov.** shares many features of its scalation (Table 3) with other *Nactus pelagicus* group members. It differs from most New Guinea populations (except those of western Gulf and Western Districts) by the absence of postmental scales (PostM). It also possesses many more tubercles (47 TubRow) in the dorsal tubercle rows, contrasting to means of 31 or less for other New Guinea populations.

Natural history. *Nactus kunan* **sp. nov.** is known from the two types; both specimens were collected within a hundred meters of each other along a forested ridgeline on the south side of the Lauis River. The two animals collected were on two different village house structures in small openings in the forest at night at approximately 200 m elevation. Surveys were conducted for more individuals for another couple of hours and no additional specimens were detected. Additionally a week of surveys in other areas north and east of this site on Manus Island, and surveys on Los Negros and Pityilu Islands all failed to detect any further individuals of this species.

TABLE 3. Summary of variation in select meristic characters in adult samples of the *Nactus pelagicus* species group. Median ± 1 standard deviation, range, and statistically significant dimorphism * (Student's t $p \leqslant 0.05$); sample size in brackets.

TAXON	SUPLAB	POSTM	DORSTUB	TUBROW	FOREFLM	HINDFLM
Nactus pelagicus (Fiji Ids)						
females [27]	4±0.50	10±2.51	18±1.47	27±1.66	19±1.01	22±1.16
	3–4	6–16	16–21	23–30	17–20	20–25
Nactus pelagicus (Admiralty Ids.)						
females [21]	4±0.59	10±3.01	15±1.57	33±2.48	20±0.97	25±1.37
	3–5	8–18	12–19	28–37	19–22	21–26
Nactus kunan **sp. nov.** (Manus Isl.)						
females [1]	5	0	17	47	18	20
Nactus galgajuga (Australia)						
adults [5]	4±0.57	11±1.93	12±0.84	22±2.07	14±0.74	17±0.95
(4 females)	3–5	8–14	10–13	20–26	13–15	16–19
Nactus eboracensis (Australia)						
females [25]	4±0.51	12±2.70	14±0.87	23±4.50	15±1.22	19±1.42
	3–4	8–20	13–16	15–34	12–17	16–21
males [34]	3.5±0.51	14±3.69	15±1.39	24±3.64	14±0.97	18±1.52
	3–4	10–24	12–18	19–35	12–16	25–22
Nactus multicarinatus (Vanuatu)						
females [35]	3±0.13	14±4.64	17±1.31	27±2.98	17±1.15	21±01.04
	2–4	2–22	14–19	22–33	14–19	19–23
males [26]	3±0.31	14±4.27	16±1.82	28.5±3.01	17±1.05	21.5±0.99
	3–4	8–22	13–20	19–33	15–19	20–23
Nactus sp[1] (Madang Province)						
females [27]	3±0.50	10±5.62	18±1.49	31±3.33	17±1.00	21±1.58
	3–4	0–22	16–22	22–35	15–19	19–25
males [24]	3±0.44	12±3.48	18±1.24	29±2.65	17±1.00	21±1.37
	3–4	4–18	15–20	25–35	15–19	19–24

[1] Three *Nactus pelagicus* group morphotypes occur in the coastal lowlands of Madang Province. We selected the most abundant morphotype for comparison with the Admiralty Islands' populations. The selected morphotype displays sexual dimorphism in SVL, TrunkL, SnForel, HeadL, and PmLab.

Nactus pelagicus (Girard) – Admiralty Islands

Description. The following description derives solely from the Admiralty sample of adults (n = 21). A moderate-sized, unisexual *Nactus* with adults ranging from 49.1–61.1 mm SVL (Table 2), 18.1–25.2 mm (mean 21.7 mm) TrunkL, 20.3–25.1 mm (24.0 mm) SnForel, 13.2–16.8 mm (15.3 mm) HeadL, 8.5–12.0 mm (10.9 mm) JawW, 5.2–7.7 mm (6.9 mm) HeadH, 2.9–4.3 mm (3.7 mm) EyeD, 4.2–5.6 mm (4.9 m) NarEye, 3.4–5.1 mm (4.0 mm) Interorb, and 2.0–2.5 mm (2.3 mm) SnW.

Body proportions are: 32–42% (29%) TrunkL/SVL, 37–46% (42%) SnForel, 25–30% (27%) HeadL/SVL, 16–21% (19%) JawW/SVL, 57–78% (70%) JawW/HeadL, 6–8% (7%) EyeD/SVL, 17–29% (24%) EyeD/HeadL, 31–34% (32%) NarEye/HeadL, 23–30% (26%) Interorb/HeadL, 13–17% (15%) SnW/HeadL.

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal trapezoidal rostral scale without middorsal notch, cleft on midline of middorsal half and distinctly depressed on its mid-posterior two-thirds; 3–4 large supralabials (Suplab) and 3 infralabials (Inflab) in front of anterior edge of orbit, first supralabial and second infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal, and posteriorly 2–3 granular loreal scales, dorsalmost one largest (>2X). Supranasals moderate sized, rectangular to semilunate in contact on midline. Scales on outer edge of eyelid slightly enlarge forming low crenate border. Chin with large trapezoidal mental and small to medium-sized postmentals (PostM = 8–18). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape unto tail; on trunk rows reach ventrolaterally to edge of venter, 12–19 entire rows (DorsTub), and only to mid-laterally on neck; tubercles in each row usually separated by one or two granular scale yielding 28–37 tubercles per row (TUBROW); 8–10 rows transversely between hindlimbs (TUBHIP). No tubercles on dorsal surface of forelimb; hindlimb with numerous tubercles (TubHindl usually 2), and tubercles density low fore and aft (TubDens = 0). Tail base with tubercle rows dorsally and laterally. Tail covered with uniform small keeled scales dorsally and ventrally (Subcaud = 0). One or 2 cloacal spurs (CloacS); distal edge usually truncate (CST = 0). Ventral scales from chin to vent small, granular and variable surfaced, smooth to weakly bicarinate. Forefoot with narrow digits, their lengths typically 2≈3>4>1≈5; 18–21 lamellae beneath fourth digit (4FingLm), 6–7 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths usually 3>2≈4>5>1; 21–26 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as row of greatly enlarged scales.

In preservative, ground color medium brown with narrow dark brown transverse bars on neck to base of tail; bars usually bordered posteriorly by narrow beige bar. Venter uniform medium brown from chin to base of tail.

Comparison to Fijian *Nactus pelagicus*. With a sample (*n* = 21) composed entirely of females and collected by multiple collectors over several decades, we propose that the most abundant Admiralty *Nactus* is an alien species and, specifically, is *N. pelagicus*. The earliest collection for this morphotype in the Admiralties is 1969 (see below in following section).

Our comparison of the Admiralty sample is limited to a Fijian one. Fiji is the origin of the type series of *N. pelagicus*, roughly in the center of the *N. pelagicus* distribution, and has a morphology characteristic of *N. pelagicus* taxon (Zug & Moon 1995). In mensural features (Table 2), the Fijian and Admiralty samples are generally similar or identical in means. The proportions offer the easiest comparison and more readily reveal differences. TrunkL/SVL (Fiji mean 42% vs. Admiralty 38%), EyeD/HeadL (28%, 23%), and Interorb/HeadL (31%, 26%) are the only proportional traits with means differing by more that 2%. These differences might suggest derivation of the two samples from different taxa; however, the number of similarities suggests otherwise, and the result is potentially due to sampling differences or measurement differences (Fijian sample measured in early 1990s, the Admiralty sample January 2011). While EyeD/SVL (7.5%, 6.5%) does not display a great difference in eye size, the EyeD and Interorb size relative to HeadL does indicate some difference in head morphology between the Fijian and Admiralty samples. This difference in comparison to the high similarity of the two samples seems inadequate to negate our hypothesis that the Admiralty '*pelagicus*' is an introduction from Oceania.

Emerging relationships among *Nactus pelagicus* group populations

The *Nactus pelagicus* complex is a Pacific Basin group of primarily ground dwelling nocturnal lizards. *Nactus kunan* was a surprising discovery on Manus Island. Our survey of available specimens revealed 33 specimens (Appendix: Specimens examined) of the typical *N. pelagicus* morphotype from the Admiralty Islands. All specimens that could be accurately sexed were females (21 adults, 8 immatures); the remaining four individuals were poorly preserved and all immature, i.e., SVL less than the minimum SVL of the 21 adults. A comparison of these adults with a sample of Fijian *N. pelagicus* shows no differences. We conclude from this similarity that the most abundant *Nactus* species in the Admiralty Islands is an invasive. We hypothesize that *N. pelagicus* arrived in the Admiralties during or immediately post WWII, as we found no earlier records of this species in these islands. Hediger (1933) was the first to list the fauna of this region and included only one *Nactus pelagicus* from New Hanover and none from either the Admiralties or St. Matthias Islands. The first record for the Admiralties that we are able to verify is Cogger's specimens from 1969, then one specimen from F. Parker in 1972, later followed by B. Mys' specimens from 1985, lastly a specimen from Rodda in 1990 (AMS, MCZ, IRSNB, and USNM, respectively in Appendix 2). *N. 'pelagicus'* was first reported from the St. Matthias Group by Brown (1955) based on specimens collected in 1944, and this remains one of the least studied island groups in the Papuan Region. Schleip (2008) discussed the *Leiopython* from the St. Matthias group and proposed that they are not endemic (contra Hoser 2000). A further assessment of the composition and morphological variation may lead to a better resolution of the biogeography and systematics of this fauna. We further hypothesize that *N. pelagicus* has **not** displaced *N. kunan* **sp. nov.** from strongly anthropogenic habitats. Ecological data for both species is inadequate to predict the potential for competition of these two species in secondary and primary forest situations and whether *N. kunan* **sp. nov.** will persist where forest are minimally disturbed or undisturbed. All *N. pelagicus* were collected in low elevations near the coast in strongly modified habitats, unlike *N. kunan* **sp. nov.** which is only known from the central forest area of Manus Island.

At this time, our data for New Guinea and associated islands indicate that *N. pelagicus* occurs only in the Admiralty's. Moritz (1987) showed that the Bismarck Archipelago contained bisexual species of the *N. pelagicus* complex. Gorge Zug's Bismarck data (*n* = 102) contains both males and females, although some localities appear to have a preponderance of females, and emphasize the necessity of a careful evaluation to determine if *N. pelagicus* has been introduced in some coastal areas. Of the MVZ specimens reported from Emirau in the St. Matthias group (Brown 1955), two are adult males, and a USNM Emirau specimen is also an adult male.

The discovery of two species on Manus Island leads to two questions: How many species of *Nactus* occur in the Pacific region and in the New Guinea area? Is the *N. pelagicus* species group a monophyletic lineage? We can offer only a preliminary assessment of the former question and outline the developing consensus on the latter question.

Prior to 1980, a small (*N. vankampeni*) and two large (*N. pelagicus*, *N. galgajuga*) *Nactus* represented the recognized diversity of this genus in the entirety of the Pacific. Moritz (1987) demonstrated a minimum of five (one unisexual, four bisexual) populations within the *pelagicus* morphotype. He offered no name assignments. Zug and Moon (1995) initiated a morphological study of the Pacific unisexual populations and the Vanuatu-Solomons bisexual populations. Their study resulted in the assignment of the nomen *pelagicus* to the Oceania populations of the unisexual *Nactus* and *multicarinatus* to the bisexual populations of Vanuatu and the southern Solomon Islands. Simultaneously, Donnellan and Moritz (1995) demonstrated the presence of four genetic groups of bisexuals (Moritz 1987): Vanuatu to north coast of Papua New Guinea (to ~ 145°45'E); north coast of PNG (~ 141° to 146°E); Southern Highlands; and coastal central Cape York Peninsula, Australia. Donnellan and Moritz assigned no specific names to these four genetic groups, although they noted that the widespread one potentially bore the name *multicarinatus*. In a subsequent study of the morphological variation within the Australian *N.* '*pelagicus*,' Zug (1998) recognized the presence of two species and resurrected the names *cheverti* and *eboracensis*, respectively, for the southern and northern Cape York entities. In 2005, Kraus reported on his discovery of two miniature *Nactus (N. acutus*, *N. sphaerodactyloides*) from islands east of Milne Bay, PNG. Morphologically, they appeared related to *N. vankampeni* and a phylogenetic analysis based on morphology revealed the two species were sister taxa and together were sister taxa of *N. vankampeni*. Kraus's analysis also revealed that the *vankampeni* group was the sister group of *N. pelagicus*, *N. multicarinatus*, and a PNG *N. pelagicus* group members. Further, his analysis indicated that *N. cheverti* and *N. eboracensis* were not closely related to PNG *pelagicus* group members and that *N. galgajuga* was even more distantly related. A subsequent study (Jackman *et al.* 2008) with nuclear and mitochondrial DNA data examined the relationships among *Dixonius*, *Heteronotia*, and *Nactus*. Their study included only a small set of *Nactus* populations; nevertheless, it demonstrated that a Lakemba drainage bisexual '*pelagicus*' population was not closely related to unisexual *N. pelagicus*. Using an expanded species data set, they (Heinicke *et al.* 2010) obtained a better resolved phylogram, demonstrating a close sister relationship for *N. pelagicus* and *N. multicarinatus* and a relationship of the preceding sister pair to the sister pair of *N. cheverti* and *N. galgajuga*. *N. eboracensis* and the Lakemba population population (possibly one of Moritz's 1987 Port Moresby types, and/or the Donnellan and Moritz (1995) group II species) were a sister pair although distantly so and on a separate and distant branch from *N. cheverti* and *N. galgajuga*. One significant aspect of this analysis, at least from our perspective, is the evidence for the monophyly of both the *N. pelagicus* species group and the *N. vankampeni* species group, although not supported by the mtDNA data alone.

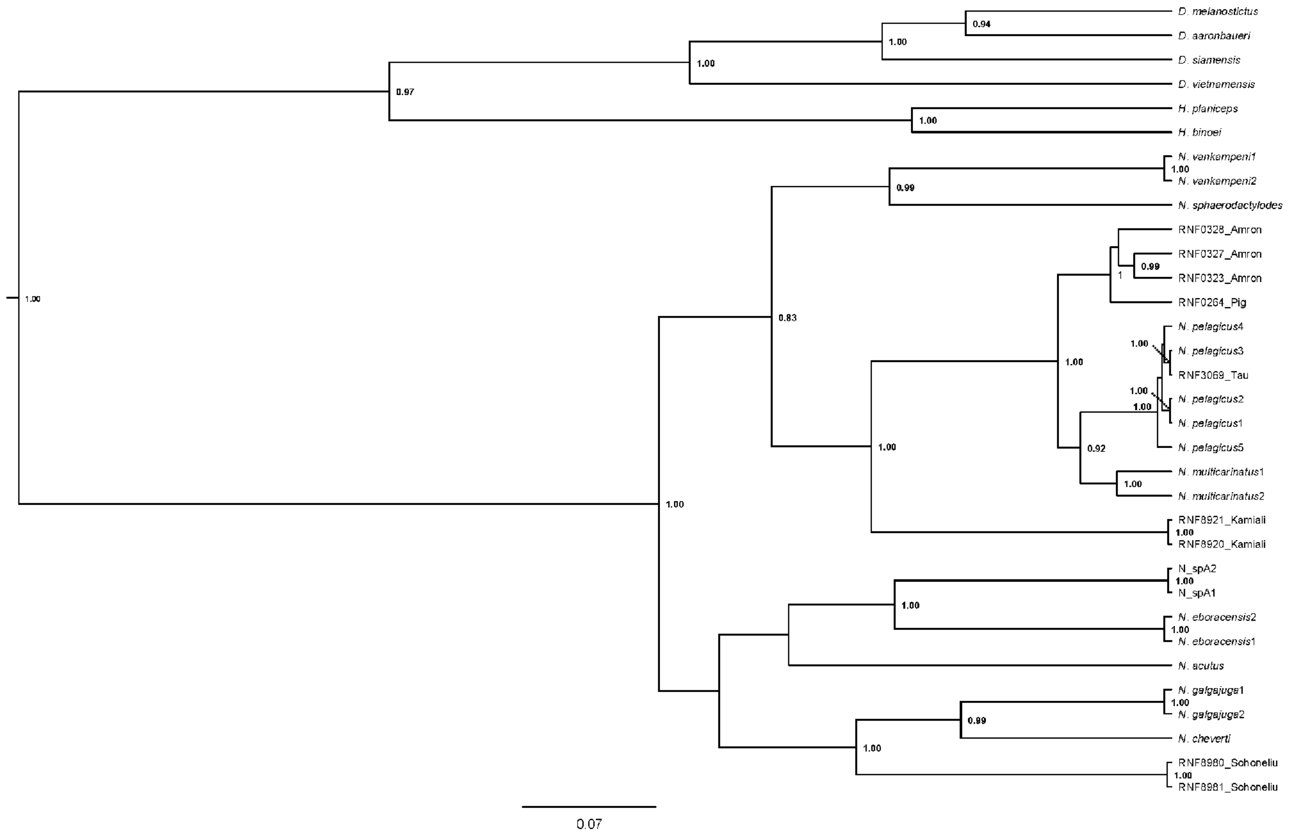

FIGURE 2. Bayesian phylogram for *Nactus* inferred from published and newly generated mitochondrial DNA sequence data (ND2; 740 bp). Table 4 lists the novel sequences; all others were from Genbank and previously reported in Heinicke *et al.* (2010). Numbers on the branches indicate posterior probabilities (PP) greater than 0.80 (PP> 0.95 are considered statistically well-supported). Strong support was received for the relationship between *N. kunan* **sp. nov.** and the two Australian species (*N. cheverti, N.galgajuga*), and the broader *pelagicus* group including samples from Madang and north coast Morobe Province.

The preceding analyses reveal considerable, presumably old, divergences within the *N. pelagicus* group and also indicate two Australia-New Guinea dispersal events, although not revealing the direction of the dispersal. We added several additional populations to the dataset generated by Heinicke *et al.* (2010). Their sampling lacked any '*pelagicus*' from the north coast of New Guinea, where Donnellan and Moritz (1995) found big breaks in their allozyme dataset. We added representatives along that coast, including coastal and inland Madang, where they saw evidence of admixture of sexual populations. Our molecular techniques and analyses are presented in the Appendix, section 1. The addition of more populations (Table 4), including *N. kunan* **sp. nov.**, results in the same tree structure as presented in Heinicke *et al.* (2010) but now with additional well supported branches, again confirming previous studies on the greater species diversity in New Guinea (Fig. 2, 3). Significantly, the monophyly of the *pelagicus* group and the *vankampeni* group is supported by the nuclear but not the mitochondrial data, whereas the occurrence of two dispersal events into Australia from New Guinea is supported by both. Especially fascinating is the well supported sister relationship of *N. kunan* **sp. nov.** with the *cheverti-galgajuga* sister pair (Fig. 2, 3), a split which was estimated to be about 11 Ma (Heinicke *et al.* 2010). This relationship probably dates from a very different configuration of the outer arc and Australia, and identifies a previously unmentioned link between Manus and Australia, and of a significant age if the dating in Heinicke *et al.* (2010) is correct. *Nactus eboracensis* and the Lakemba population retain a sister relationship but distantly. Madang individuals show great diversity, even within the population in the Adelbert Range (Amron), and versus the coastal individual (Pig Island). Both phylograms support the clade that includes the Madang specimens, *multicarinatus*, and *pelagicus*, such as was first identified by Donnellan and Moritz (1995) as their group IV. The formerly unsampled Morobe coast shows very deep divergence between this population (Kamiali Biological Research Station) and Madang '*pelagicus*" (?= *multicarinatus*), although in both phylograms, the clade that includes all of these is always supported.

FIGURE 3. Bayesian phylogram for *Nactus* inferred from published and newly generated nuclear DNA sequence data (RAG-1 and PDC; 639 bp combined). Table 4 lists the novel sequences; all others were from Genbank and previously reported in Heinicke et al. (2010). Numbers on the branches indicate posterior probabilities (PP) greater than 0.80 (PP> 0.95 are considered statistically well-supported). Strong support was received for inclusion of *N. kunan* **sp. nov.**, *N. cheverti*, *N. galgajuga*, with the broader *pelagicus* group including samples from Madang and north coast Morobe Province to the exclusion of the '*vankampeni*' group (*N. acutus*, *N.sphaerodactylodes*, *N. vankampeni*). These findings are consistent with the significant ones determined by Heinicke *et al.* (2010).

Other relationships are revealed in our phylograms (Fig. 2, 3); however, we believe the absence of many of the unrecognized New Guinea species produces an unreliable tree as so many branches are missing. That impression of unreliability returns us to the question of how many *Nactus* species reside in New Guinea and adjacent islands. We cannot give a definitive answer now, although ongoing morphological data-gathering allow us to offer the following enumeration as a tentative assessment, presented without morphological support.

Beginning in the Vogelkop, Rösler and collaborators (2005) reported on three recently collected specimens. All three were identified as their Form B. Our assessment of these *Nactus* is that they represent two species: one from the Wondiwo Mtns. and the second from the Nibire-Mapia corridor at the base of the Vogelkop neck. Possibly, one of these species represents *N. arfakianus* (Meyer). A huge hiatus exists from these few specimens to samples from the Humboldt Bay-Vanimo area and another species. East of the Sepik R. to the Huon Peninsula, there are two morphotypes in the coastal samples and potentially a third one (our Madang samples represent at least one of these). The situation from the Huon Peninsula to Collingwood Bay area (including the Bismarck Archipelago) is still unclear although a large rainforest species (Kamiali sample) appears surrounded by a moderate-sized species. In the Milne Bay area, we are able to recognize two mainland species and a minimum of six insular species, one of which may be shared with the mainland. Westward along the south coast, a savanna-scrub species (Macleay's Hall

Sound species) and a rainforest species occur in the Port Moresby area. The westward extent of the rainforest species has not been delimited, nor is it clear whether it is the same as the genetically distinct Lakemba population (Heinicke *et al.* 2010). Our uncertainty of diversity within the western Gulf and Western Districts results from few specimens and presently incomplete analysis. No specimens are available from the south coast of Papua-Indonesia. It seems likely that the Kei population (*undulatus*) represents an endemic *Nactus*. This overview of diversity within the New Guinea *Nactus pelagicus* group suggests at least 16 species, a diversity more in keeping with the complex geological history of the island. We also have determined that potential invasion of asexual *N. pelagicus* may be a factor in obscuring historic patterns of diversity, and a combination of morphological and molecular approaches will be necessary to resolve these patterns.

TABLE 4. Specimens used for genetics in this study. Abbreviations are as follows: USNM = United States National Museum, PNGNM = Papua New Guinea National Museum, CAS= California Academy of Sciences.

SPECIES	IDENTIFICATION NUMBER	LOCALITY	GENBANK ACCESSION NUMBER		
			ND2	RAG-1	PDC
Nactus kunan 1	USNM 576300 [RNF8980]	PNG[1], Manus Island, Sohoniliu village	JQ627857	JQ231297	JQ627849
Nactus kunan 2	PNGNM 25190 [RNF8981]	PNG, Manus Island, Sohoniliu village	JQ627858	JQ231298	JQ627850
Nactus Kamiali 1	USNM 576310 [RNF8919]	PNG, Morobe Prov., Kamiali village	-	JQ231294	JQ627846
Nactus Kamiali 2	CAS 249851 [RNF8920]	PNG, Morobe Prov., Kamiali village	JQ627859	JQ231295	JQ627847
Nactus Kamiali 3	PNGNM oooo [RNF8921]	PNG, Morobe Prov., Kamiali village	JQ627856	JQ231296	JQ627848
Nactus '*pelagicus*'[2] 1	CAS 192884 [RNF323]	PNG, Madang Prov., Amron village	JQ627852	JQ231290	JQ627842
Nactus '*pelagicus*' 2	CAS 192887 [RNF327]	PNG, Madang Prov., Amron village	JQ627853	JQ231292	JQ627843
Nactus '*pelagicus'* 3	CAS 192888 [RNF328]	PNG, Madang Prov., Amron village	JQ627854	JQ231291	JQ627844
Nactus '*pelagicus*' 4	CAS 192903 [RNF264]	PNG, Madang Prov., Madang (Pig Island)	JQ627851	JQ231299	JQ627841
Nactus pelagicus	CAS 235707 [RNF2069]	American Samoa, Tau Island	JQ627855	JQ231293	JQ627845

[1] PNG is an abbreviation for Papua New Guinea

[2] *Nactus* '*pelagicus*' designates un-named bisexual species of the *N. pelagicus* species groups. There are potentially two species in Madang Province, possibly a coastal species and an upland one that may co-occur in the same area, although not necessarily microsympatrically.

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The collections management staffs of numerous museums have greatly aided our examination of members of the *Nactus pelagicus* species group. We appreciate this assistance and thank: D. Kizirian, R. Pascocello, and D. Dickey, American Museum of Natural History (AMNH); R. Sadlier, Australian Museum-Sydney (AMS); C. McCarthy, The Natural History Museum, London (BMNH); C. Kishinami and K. Imada, Bernice P. Bishop Museum (BPBM); J. Vindum, California Academy of Sciences (CAS); G. Lenglet, G. Coulon, Institut Royal des Sciences Naturales de Belgique (IRSNB); J. Rosado, J. Woodward, Museum of Comparative Zoology, Harvard University (MCZ); P. Couper, Queensland Museum of Natural History (QM); G. Schneider, University of Michigan Museum of Zoology (UMMZ); and S. Gotte, J. Jacobs, K. Tighe, and R. Wilson, National Museum of Natural History, Smithsonian Institution (USNM).

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Appendix

Specimens examined

Unisexual population.

Nactus pelagicus [Fiji Islands]: CAS 102362-363, 159940, 171903-904, 171906, 171940-947; UMMZ 183217; USNM 5626, 22985-896, 229981, 230088, 230264-265, 267930-932, 268180-181, 268186.

Nactus pelagicus [Manus Island]: AMS R29071-074, R3114-115; IRSNB 16840.3623-625, 16840.3750-51, 16840.3759-60, 16840.3820-22, 16840.3859, 16840.3861-75; MCZ R139531 [photograph only]; USNM 566887.

Bisexual populations.

Nactus eboracensis [Australia]: AMS R38526, R56040, R56043, R56045-046, R56048, R56059, R56215, R56287, R581923, R69938-940, R81923, R94021-024, R94026, R94104-106, R94144, R94154, R94171, R94508, R99935-936, R99938, R105129-135, R105142, R126033; MCZ R124298, R137658-659, R140953; QM J26687, J34466-468, J34537, J38103, J38105, J38460-461, J38464, J39767, J39789, J58211.

Nactus galgajuga [Australia]: AMS 570110; QM J29474, J52973, J61071, J61095; USNM 561888-890, 561892-893.

Nactus kunan **sp. nov.** [Manus Island]: PNGNM 25190 (RNF8981); USNM 576300.

Nactus multicarinatus [Vanuatu, Efate & Espiritu Santo]: AMNH 41908-909, 41911-915, 41917-918, 81604-607, 81610-18; BMNH 71.4.16.35, 71.4.16.41A-C; CAS 171911-913, 171915, 171917-919, 171924-925, 171929-930, 171932-938; MCZ R47144, UMMZ 99999A-C, 99999L-M; USNM 119631-640, 122168-169.

Nactus ‘pelagicus’ [Madang area]: AMS R31260-262, R31268, R31272, R31278, R31281, R31284, R31291-292, R31297, R6124050, R124052-053, R124018-022, R124024-030; BPBM 31467, BPBM.JW18-19, BPBM.JW48; CAS126710-711, 126713, 134376-378; IRSNB 16456A-G; MCZ R101533, MCZ R24293-295, MCZ R124302-304.