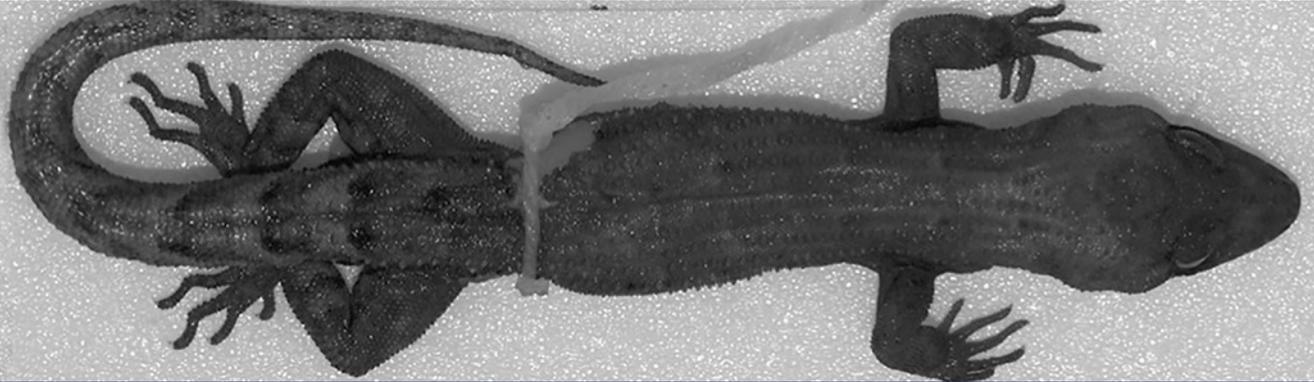




Smithsonian
Scholarly Press

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 651



Diversity in Pacific
Slender-Toed Geckos,
Nactus pelagicus Complex
(Reptilia: Squamata),
of New Guinea and
Adjacent Islands

George R. Zug

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of “diffusing knowledge” was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: “It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge.” This theme of basic research has been adhered to through the years in thousands of titles issued in series publications under the Smithsonian imprint, commencing with Smithsonian Contributions to Knowledge in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Botany
Smithsonian Contributions to History and Technology
Smithsonian Contributions to the Marine Sciences
Smithsonian Contributions to Museum Conservation
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology

In these series, the Smithsonian Institution Scholarly Press (SISP) publishes small papers and full-scale monographs that report on research and collections of the Institution’s museums and research centers. The Smithsonian Contributions Series are distributed via exchange mailing lists to libraries, universities, and similar institutions throughout the world.

Manuscripts intended for publication in the Contributions Series undergo substantive peer review and evaluation by SISP’s Editorial Board, as well as evaluation by SISP for compliance with manuscript preparation guidelines (available at <https://scholarlypress.si.edu>). SISP open access publications are licensed under Creative Commons licenses based on copyright status of content. Each is published initially online at <https://smithsonian.figshare.com/ScholarlyPress> and in print format in limited quantities.

Diversity in Pacific
Slender-Toed Geckos,
Nactus pelagicus Complex
(Reptilia: Squamata),
of New Guinea and
Adjacent Islands

George R. Zug



Smithsonian
Scholarly Press
WASHINGTON, D.C.
2020

ABSTRACT

Zug, George R. Diversity in Pacific Slender-Toed Geckos, *Nactus pelagicus* Complex (Reptilia: Squamata), of New Guinea and Adjacent Islands. *Smithsonian Contributions to Zoology*, number 651, x + 92 pages, 35 figures, 9 tables, 3 appendixes, 2020. — The diversity within the genus *Nactus* is slight in comparison to the other Australasian genus of narrow-toed geckos (*Cyrtodactylus*). The latter now has more than 290 species, with over half of these species newly described in the twenty-first century. In contrast, prior to this study, 12 *Nactus* species were recognized formally in the recent herpetological literature: three species in the Mascarene Islands, two in the Pacific Islands, three in Australia, and six in New Guinea and associated island groups. Three of these New Guinea species are miniature (snout–vent length ≤ 40 mm) species, and three are in the *pelagicus* complex; with the exception of the recently described *N. kunan*, all other New Guinean populations were labeled *N. pelagicus* even though they were known to be bisexual species and differed from the unisexual *N. pelagicus* of Oceania. Considering only bisexual New Guinean “*pelagicus*,” my morphological analyses recognize 24 distinct populations for which I provide new names or resurrected species names from synonymies. Of these 24, two species are extralimital (Morotai and Kei Islands). The sampling of *Nactus* in Indonesia Papua is very poor, with only one specimen from the base of the Vogelkop, two from south coast drainages, and more than a dozen from islands from the east coast of Cenderawasih Bay; the remainder derive from Papua New Guinea (PNG). The Indonesia Papua populations represent four species, two of which are shared with PNG. Papua New Guinea thus has a total of 20 species, varying from widespread species (e.g., north coast of main Papua to the Sepik-Ramu area) to a single locality in Madang or single islands in the Louisiade Archipelago. Most distributions of the PNG species match at least one other PNG anuran or reptile species. The greatest diversity of PNG species occurs in Madang Province to Huon Peninsula and the Milne Bay mainland with sympatry in both areas. The “*pelagicus* complex” of species is herein confirmed to be polyphyletic. In spite of its use in this study, its subsequent use should be restricted to the unisexual species and their parental species, of which only one (*N. multicaudatus*) is known. The preceding represents a subgroup within the larger clade of Australian and New Guinean bisexual species. For the present, I do not recommend a name for this group because a molecular phylogenetic analysis will be required to identify the cladogenesis of the *Nactus* species.

Cover image: Detail from Figure 27, holotype of Milne Bay Pygmy Slender-toed Gecko *Nactus chrisaustini*, new species (LSUMZ 123550) in dorsal view; photo by G. Zug.

Published by SMITHSONIAN INSTITUTION SCHOLARLY PRESS
P.O. Box 37012, MRC 957, Washington, D.C. 20013-7012
<https://scholarlypress.si.edu>

Compilation copyright © 2020 Smithsonian Institution

The rights to all text and images in this publication, including cover and interior designs, are owned either by the Smithsonian Institution, by contributing authors, or by third parties.



This work is licensed under a Creative Commons Attribution-NonCommercial 4.0 International (CC BY-NC 4.0) License.

Library of Congress Control Number: 2020937994

ISSN: 1943-6696 (online); 0081-0282 (print)

ZooBank registration: 28 September 2020 (LSID: [urn:lsid:zoobank.org/pub:8C2CDF02-439B-4DA2-91FD-807FD628F9F0](https://zoobank.org/pub:8C2CDF02-439B-4DA2-91FD-807FD628F9F0))

Publication date (online): 14 October 2020

⊗ The paper used in this publication meets the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48–1992.

Contents

LIST OF FIGURES	v
LIST OF TABLES	vii
PREFACE	ix
INTRODUCTION	1
History of Discoveries in Australo-Pacific <i>Nactus</i>	1
MATERIALS AND METHODS	4
MORPHOLOGY AND VARIATION	6
Sexual Dimorphism	6
Measurements	8
Body Size	8
Head Size and Shape	12
Scalation	16
Head	17
Body and Limbs	23
GEOGRAPHY, RELATIONSHIPS, AND TAXONOMY	25
Genetic Lineages	25
Discrimination of Unisexual and Bisexual Populations	27
Geographic Patterns of Morphological Variation	27
Geography of Size and Shape	27
Geography of Scalation	27
Taxonomic Decisions	31
Species Accounts – New Guinea Region	37
DIVERSITY AND DISTRIBUTION PATTERNS IN THE NEW GUINEAN HERPETOFAUNA	72
ACKNOWLEDGMENTS	76
APPENDIX A: CHARACTER DEFINITIONS	79
APPENDIX B: SAMPLE NUMBERS, GEOGRAPHIC NAMES, AND SPECIMENS EXAMINED	81

APPENDIX C: SPECIES IDENTIFICATION OF INDIVIDUALS EXAMINED	85
REFERENCES	87
INDEX OF SCIENTIFIC NAMES	91

Figures

1. Distribution of samples within the New Guinea region	5
2. Frequency distribution (histogram) of average body size (SVL)	12
3. Frequency distribution of head size (HeadL/SVL percentages)	16
4. Head scale morphology in <i>Nactus pelagicus</i> complex geckos	17
5. Schematic illustration of variation in postmental scale morphology	18
6. Association of the number of dorsal tubercle rows and number of tubercles in a parasagittal row of tubercles	23
7. Schematic representation of tubercle traits of the hindlimbs of New Guinea <i>Nactus pelagicus</i> group members	23
8. Variation in hindlimb enlarged tubercle distribution and density	24
9. Schematic illustration of the underside of <i>Nactus</i> tail	25
10. Generalized dendrograms of hypothetical genetic relationships among samples of southwest Pacific <i>Nactus</i> populations	26
11. Holotype of <i>Nactus arceo</i> (BYU 7540)	37
12. Occurrence of <i>Nactus</i> species in western New Guinea	39
13. An individual of <i>Nactus arfakianus</i> (UMMZ 122449) from Numfoor Island	40
14. Holotype of <i>Nactus rainerguentheri</i> (ZMB 62760)	40
15. Holotype of <i>Nactus septentrionalis</i> (USNM 119240)	41
16. Holotype of <i>Nactus allenallisoni</i> (AMS R31261)	42
17. Holotype of <i>Nactus nanus</i> (AMS R124053)	46
18. Occurrence of <i>Nactus</i> species in northern coastal region and Manus Island, Papua New Guinea	47
19. Holotype of <i>Nactus intrudusus</i> (AMNH 95175)	48
20. Holotype of <i>Nactus robertfisheri</i> (BPBM 22014)	50
21. Holotype of <i>Nactus kamiali</i> (BPBM 25964)	51
22. Occurrence of <i>Nactus</i> species in northern peninsula mainland and islands, Papua New Guinea	53
23. Holotype of <i>Nactus fredkrausi</i> (BPBM 16749)	55
24. Holotype of <i>Nactus panaeati</i> (AMS R4777)	56
25. Holotype of <i>Nactus modicus</i> (BPBM 19852)	57
26. Holotype of <i>Nactus amplus</i> (BPBM 19864)	59
27. Holotype of <i>Nactus chrisaustini</i> (LSUMZ 123550)	60
28. Holotype of <i>Nactus notios</i> (LSUMZ 123547)	61
29. Paratype of <i>Nactus erugatus</i> (BPBM 15450)	63

30. Holotype of <i>Nactus alotau</i> (BPBM 15849)	64
31. Topotype of <i>Nactus heteronotus</i> (USNM 325082)	66
32. Occurrence of <i>Nactus</i> species on the south coast of Papua New Guinea	67
33. Holotype of <i>Nactus papua</i> (CAS 118023)	68
34. Holotype of <i>Nactus inundatus</i> (USNM 325059)	69
35. Holotype of <i>Nactus undulatus</i> (RMNH 5095)	71

Tables

1. Traits displaying dimorphism and their frequency of occurrence in New Guinea <i>Nactus pelagicus</i> group samples	7
2. Distribution and frequency of precloacal pores in adult females and males in the New Guinea <i>Nactus pelagicus</i> group samples	7
3. Select body size traits and their variation in adults of New Guinea <i>Nactus pelagicus</i> group samples	9
4. Select head size traits and their variation in adults of New Guinea <i>Nactus pelagicus</i> group samples	13
5. Select scalation traits and their variation in juveniles and adults of New Guinea <i>Nactus pelagicus</i> group samples	19
6. Distribution of tuberculate and nontuberculate hindlimbs (TubHindl) among the New Guinea <i>Nactus</i> samples	28
7. Comparison of northeastern coast samples of <i>Nactus</i> in which the subcaudal scales are keeled	35
8. Summary of character states for differentiation of New Guinea bisexual species of medium to large <i>Nactus</i>	38
A1. Abbreviations and definitions for characters examined	80

Preface

Serendipity has ruled my research career and my life in general. As a small-town boy headed for Penn State's forestry school, I was convinced by my weekend employer—a retired Pennsylvania state forester—that forestry was not a good choice. That decision led to my enrollment at Albright College and to the tutelage of Al Schwartz. I had no previous interest in amphibians and reptiles until working with Al in the field and lab. Through those interactions, I developed a fascination with herps and systematics. That fascination eventually led me to the Smithsonian. A question was put to me by a 1970 visitor working in our division library: Did I know of anyone who might trade houses and research spaces with him? The question was quickly answered, and in September 1971, Pat, the kids, and I were settling into a house in the Boroko-Port Moresby area of Papua New Guinea for a five-month stay. My research office was at the Moitaka Wildlife Laboratory surrounded by supportive colleagues and saltwater crocodiles.

Port Moresby and its associated suburbs lie within a coastal savanna of low hills abutting the rugged Owen Stanley mountain range and its forests. My initial fieldwork was in this savanna. I soon—well, when the rains began—found a specimen of a small *Nactus* in a patch of scrubby forest in the savanna. Collecting in the evergreen forest near the mountains, I found a larger and darker *Nactus*. These discoveries and subsequent ones as I traveled around Papua New Guinea sparked my research interest in *Nactus* diversity.

Returning to the Pacific in 1984, I again found *Nactus* regularly in the heaps of rotting coconut husk in Fiji. We recognized then that the population of *Nactus* in American Samoa was an all-female population, hence likely parthenogenetic based on Terry Schwaner's reproductive study (1980) of the Samoan lizard fauna. My samples from various Fijian islands and subsequently from Upulo, Samoa, comprised only females, strengthening the conviction that *N. pelagicus* from the central Pacific was a unisexual species. This assumption was examined by Moritz (1987); he demonstrated that unisexual *Nactus* populations occurred from New Caledonia and southern Vanuatu eastward into the south central Pacific. Using allozymes and karyotypes, he demonstrated further that multiple differentiated populations of *Nactus* existed in the southern Pacific Rim islands and Australia. The latter data encouraged Brad Moon and me to begin a morphological examination of bisexual and unisexual populations. Our intent was to define morphologically Moritz's genetically delimited populations. Casting our research net broadly, we quickly discovered that there was more morphological divergence than identified by Moritz's study and broader sampling would be required. The initial focus was

to delimit morphological variation in the unisexual populations and the abutting or sympatric bisexual populations of Vanuatu (Zug and Moon, 1995). Graduate school called, and Brad moved on to functional morphology. I slowly began to expand my samples, geographically and numerically. Not surprisingly, this activity revealed an even greater diversity in bisexual populations. I gnawed at the edge of this diversity with an examination of Australian populations (Zug, 1998) of what had become by then the *Nactus pelagicus* complex. New Guinea harbored even greater diversity and, of course, more difficulties in delineating and understanding this diversity. The following study offers a first swipe at recognizing this broader diversity and, I hope, provides a substantial baseline for colleagues to build upon.

Diversity in Pacific Slender-Toed Geckos, *Nactus pelagicus* Complex (Reptilia: Squamata), of New Guinea and Adjacent Islands

George R. Zug

INTRODUCTION

Most *Nactus pelagicus* group geckos are cryptically colored inhabitants of forest floors. Their brown background color dabbled with darker chevron-shaped bars and blotches with smaller flecks of cream and beige serves as an excellent camouflage amid forest floor debris. This crypsis has also hidden them from the attention of field naturalists and systematists. For much of the twentieth century, their diversity was hidden beneath two or three names. With the discovery that the populations of *Nactus pelagicus* in Oceania were all females (Schwaner, 1980), they became evolutionarily more fascinating and have attracted a little more research attention to their biology, relationships, and taxonomy. This study focuses on morphological variation within the New Guinea populations of medium to large members of the *N. pelagicus* group and reveals a more complex evolutionary history and greater speciation than previously assumed.

HISTORY OF DISCOVERIES IN AUSTRALO-PACIFIC *NACTUS*

Nactus is a relatively new nomenclatural paradigm, proposed in 1983 (Kluge, 1983) for the clade of narrow-toed geckos possessing fused nasal bones, a second ceratobranchial in the hyoid apparatus, and enlarged cone-shaped dorsal body tubercles. When proposed, *Nactus* encompassed four species: *galgajuga*, *pelagicus*, *serpensinsula*, and *vankampeni*. These species were previously members of the polyphyletic *Cyrtodactylus* assemblage and, even earlier, of the *Gymnodactylus* aggregate.

The first *Nactus* population to be recognized as a distinct species was described as *Gymnodactylus arnouxi* (Duméril and Duméril, 1851) and was subsequently described in more detail (Duméril, 1856). Unfortunately, the specimen had incorrect locality data, New Zealand. Duméril's name was rarely used because this gecko does not occur in New Zealand. If noted in a list of New Zealand herpetofauna, it was reported as an unconfirmed species. McCann (1955:17) forthrightly stated, "There is no authentic evidence to support the occurrence of *G. arnouxi* within the limits of the fauna [of New Zealand], and accordingly I exclude it." The possible origin of the holotype of *G. arnouxi* is addressed subsequently in the Geography, Relationships, and Taxonomy section.

In 1857, Girard described *Heteronota pelagica* from specimens collected by the U.S. Exploring Expedition in Fiji and Samoa. Girard did not report the number of specimens

Division of Amphibians and Reptiles, MRC162,
National Museum of Natural History, Smithsonian
Institution, P.O. Box 37012, Washington, D.C.
20013-7012, USA.

Correspondence: zugg@si.edu

Manuscript received 9 September 2019; accepted
17 April 2020

examined. Presently, only two remain. Both specimens are from Fiji, and I restricted the type locality to Ovalau, Fiji (Zug, 1985). A dozen years after Girard's description, Günther (1872) examined specimens collected by J. L. Brenchley during his travels in 1865 in the South Seas. He had specimens from two distant localities: Tongatabu, Tonga, and Anatom, Vanuatu. He noted in his 1872 description that he was providing the diagnosis from a forthcoming book by Brenchley, but a publication delay encouraged him to publish now. Brenchley's book appeared a year later and contained Günther's diagnosis of *Gymnodactylus multicarinatus* in an appendix (Günther, 1873). The texts of the two diagnoses are identical, with exception that the 1873 one contains measurements of a single specimen. To fix the name *G. multicarinatus* to a specific population, Zug and Moon (1995) designated Efate, Vanuatu, as the type locality. The reason for using Efate rather than Anatom is explained in the latter publication.

Meyer (1874) described a *Nactus* (*Gymnodactylus* (*Heteronota*) *arfakianus*) and other reptiles from his 1870 to 1873 trip to New Guinea. For many of these new species, including *G. arfakianus*, he gave only "Neu-Guinea" as the origin of the new taxon. Subsequently in 1887, he provided specific localities for all of his specimens collected during that trip. He specified "Doré" (Yapen Island) for the origin of his lone specimen of *G. arfakianus*. The type of *G. arfakianus* was housed in the Dresden Staatliches Museum für Tierkunde and was destroyed with all other Dresden specimens during World War II (Bauer and Günther, 1991).

The next New Guinean *Nactus* described was *Heteronota fasciata* from Hall Sound (Macleay, 1878) in southern New Guinea, present-day Central Province, Papua New Guinea. In the same article, Macleay also described *Heteronota eboracensis* from Cape York. No further New Guinea *Nactus* were recognized until Kopstein's description (1926) of *Gymnodactylus pelagicus undulatus* from the Kei Besar (Kepulauan Kei, Indonesia). This taxon has attracted little attention from the herpetological community, and I have found no subsequent reference to its biology or morphology.

In volume 1 of his *Catalogue of the Lizards in the British Museum*, Boulenger (1885) provided descriptive accounts for four members of the *pelagicus* group: *Gymnodactylus arnouxii*, *G. pelagicus*, *G. heteronotus*, and *G. cheverti*. Unlike his subsequent account for *G. pelagicus*, he listed no specimens from The Natural History Museum for *G. arnouxii*, and his abbreviated description derived from the earlier descriptions of A. Duméril (in Duméril and Duméril, 1851; Duméril et al., 1856). His description of *G. pelagicus* was more detailed, noting the presence of a pair of chin shields (=postmentals; but he did not mention relative size) and seven to eight preloacal pores in males. Boulenger's description was clearly based on an examination of some or all ($n = 32$) specimens that he had available in the British Museum. He synonymized *G. multicarinatus* Günther, *G. arfakianus* Meyer, and *G. arnouxii* (non Duméril and Bibron) Peters and Doria, 1878 with his concept of *G. pelagicus*. Further, he provided substitute names for Macleay's *Heteronota fasciatus*

and *H. marmorata* (*G. heteronotus* and *G. cheverti*, respectively) as the former names were junior homonyms. Boulenger's descriptions of these two latter taxa were direct quotes of Macleay's descriptions because he lacked specimens. He retained *H. eboracensis* Macleay in the genus *Heteronota*, again directly quoting Macleay's description.

Nelly de Rooij (1915) provided the first detailed description of New Guinea *Nactus pelagicus*. She had two dozen "mainland" New Guinea specimens available to her and based her description mainly on eastern Papua Indonesian specimens (presumably $n = 5$ or, at least, specimens from five localities, principally centered on the Humboldt Bay area). She noted a pair of small chin shields, 16 to 20 longitudinal rows of tubercles on the trunk, and 7 to 10 preloacal pores. Her localities delimited a distribution of *N. pelagicus* extending from western New Guinea and the Bismarck Archipelago through the Solomon and Vanuatu Islands to Tonga and Fiji.

Kopstein surveyed the Moluccas and some nearby islands from 1922 to 1924. His 1926 report listed *N. pelagicus* from 2 of the 24 regions surveyed: Kei Island and the Jakati River area at the throat of the Vogelkop of mainland New Guinea. The description of the two Jakati specimens was brief; he noted a pair of small postmentals. He described the Kei specimen as a subspecies, *N. p. undulatus*, noting the absence of postmentals, 12 longitudinal rows of trunk tubercles, and short, dark, mid-dorsal transverse bars on the trunk with narrow posterior light borders on the posterior bars.

Brongersma (1933) discovered two small adult *Nactus* specimens in a collection from northern Dutch New Guinea and described them as a new species, *Gymnodactylus vankampeni*. Aside from a smaller adult size (~30 mm snout-vent length [SVL]), this gecko lacked postmentals and had fewer longitudinal rows of tubercles on the trunk. He expressed uncertainty about the uniqueness of this taxon; however, his uncertainty has proved incorrect. *Nactus vankampeni*, although not a member of the *pelagicus* group, is a distinct and widespread species occurring over hundreds of kilometers on the north coast of New Guinea. Much later, Brongersma (1948) examined a collection of lizards from Morotai and reported that this Moluccan island had at least 19 species of lizards, one of which was a new species of *Cyrtodactylus* (then *Gymnodactylus*), although not a member of the *pelagicus* group. The discovery of *Nactus* on this island had to await the return of U.S. servicemen from New Guinean battlefields and their deposition of their small, but significant, collections in museums. One serviceman discovered two specimens of "*Gymnodactylus pelagicus*" in October 1944 (Tanner, 1950). This species has not been reported subsequently from Morotai.

Loveridge (1948) summarized the holdings of New Guinean amphibians and reptiles in the collection of the Museum of Comparative Zoology, Harvard (MCZ), and the Smithsonian's U.S. National Museum. Loveridge, as he noted in his introduction to this monograph, began the project to promulgate data from the many specimens received from American servicemen serving in New Guinea. He provided a summary of scalation traits for

a sample of 29 individuals, geographically extending from New Britain and Milne Bay to Toem, western Indonesia–New Guinea. He concluded that “*G. p. undulatus* Kopstein, from the Kei Islands does not seem too well established” owing to the absence of postmentals not being a variable trait throughout the range of *pelagicus*.

More than a decade passed before Pacific *Nactus* was mentioned again in the herpetological literature. In 1973, Brown and Parker described a new species of *Cyrtodactylus* from the upper reaches of the Fly River drainage. They noted that *pelagicus* and *vankampeni* differed from other *Cyrtodactylus* (= *Gymnodactylus*) by no or only slightly enlarged pores in the precloacal series harboring glandular pores.

Ingram’s 1978 discovery of a black-and-white-banded *Cyrtodactylus* (now *Nactus galgajuga*) from the black boulder mountains just south of Cooktown was made without any fanfare. Although its bold coloration and slender habitus would subsequently set it apart from all other *Nactus* relatives, bold contrasting colors and banding are not uncommon in the genus *Cyrtodactylus*; thus, it was just another new gecko for Australia and presumably of “minor evolutionary interest” because it was the third endemic species (in addition to a microhylid frog and scincid lizard) from this jumble of giant granite boulders.

Schwane (1980) examined reproduction of the Samoan lizards and discovered that his entire sample of *N. pelagicus* was females. He recognized the likelihood that “a parthenogenetic population of *C. pelagicus* exists on Ta’u Island.” It was this observation that led to Moritz and King (1985), who were studying unisexual populations of *Heteronotia* in Australia, to include *Nactus* in their survey of parthenogenesis. Their preliminary results indicated the presence of unisexual populations also in Fiji and New Caledonia and bisexual populations westward from Vanuatu into New Guinea and Australia. Moreover, the karyotype of unisexual *N. pelagicus* indicated a hybrid origin, with the Vanuatu bisexual likely being one of the parental species (Moritz and King, 1985: fig. 4). This figure also indicated the presence of two “species” (karyotypes) in the Port Moresby area. Moritz (1987) expanded his analysis of multiple island samples of this taxon, and his results were the keystone study that identified the potential diversity of this presumed widespread species. The key aspects were (1) demonstration of the occurrence of all-female populations broadly in the south central Pacific Islands, (2) the sympatry of uni- and bisexual populations in Vanuatu, and (3) karyotypic and allelic evidence for multiple differentiated bisexual populations in New Guinea and Australia. He offered no taxonomic changes for his demonstrations of multiple cryptic species: tropical Queensland, southeastern Papua New Guinea (PNG), and at least two allelic groups (i.e., genetically divergent) on the north coast of PNG.

Amid this recognition of the “peculiarity” of *pelagicus*’s sex life, Kluge was continuing his study of gecko phylogenetic relationships and published (Kluge, 1983) an article recognizing monophyly of a group of gekkonine geckos, the Gekkonini, by the absence of a second ceratobranchial in the hyoid

arch. Additionally, his analysis of relationships revealed that *Cyrtodactylus* was polyphyletic and that one group possessed a unique set of traits. This discovery led to his recognition of the monophyly of this group of species and the description of *Nactus* for five species (*arnouxii*, *galgajuga*, *pelagicus*, *serpensinsula*, *vankampeni*). In proposing a new genus, Kluge designated *Gymnodactylus arnouxii* Duméril and Duméril, 1851 as the type species of *Nactus*. This action led to the possible synonymization of *Gymnodactylus pelagicus* Girard, 1857; however, because *G. arnouxii* was a little-used name and its type locality is New Zealand, the Zoological Commission of Nomenclature (1991) preserved *G. pelagicus* as the name for the Pacific parthenogenetic *Nactus*.

Donnellan and Moritz (1995) continued Moritz’s earlier molecular and karyotypic study with an expansion of geographic samples and mtDNA analysis. Their results revealed both an increasing diversity of bisexual populations and the beginning of a delineation of the geographic distribution of these different bisexual entities. One bisexual defined karyotypically ($2N = 28$) occurs broadly from the northern islands of Vanuatu (Efate) to the middle of the north coast (Madang area) of PNG with members in Bougainville and northern Solomon Islands. This karyotypic group shared a common allozymic signature and eight haplotypes. Another allozyme group occurred in tropical Queensland with a $2N = 38$ karyotypic signature (subsequently identified as *N. cheverti*; Zug, 1998). Two montane PNG samples each displayed a different allozyme signature, and one of these signatures was shared with an individual from the northwest PNG coastal lowlands (Madang area). This latter sample area had two allozyme signatures. Donnellan and Moritz also discovered a hybrid between the two Madang genetic entities. Importantly, this study confirmed the presence of multiple bisexual populations (i.e., at least three allozyme groups) on the northern PNG coast. Of these groups, only one was later investigated by sequencing mitochondrial loci, and it was distinct from the Solomon and Vanuatu bisexual *Nactus*.

In the same year, Zug and Moon (1995) examined morphological variation in Oceania and Vanuatu samples. Although morphological differentiation was not striking, bisexual and unisexual populations could be differentiated. Fiji was the topotypic locality for *pelagicus*, hence the name for unisexual populations. The name *multicarinatus* was fixed for the bisexual populations of Vanuatu. The western extent of the distribution of *N. multicarinatus* was not delineated.

Later, Zug (1998) examined morphological variation in the Australian *Nactus* populations. This study revealed three morphotypes in tropical Queensland, a southern one (*N. cheverti*) from the Flinders Group southward, an eastern Cape York species (*N. eboracensis*) that extends into the eastern Torres Islands, and a southwestern PNG species (presently unidentified) on the principal arc of Torres Islands.

Kraus (2005) reported his discovery of two dwarf *Nactus* from Milne Bay Province, eastern PNG, one (*N. sphaerodactylodes*; Sudest Island) distinctly smaller than *N. vankampeni*

and the other (*N. acutus*; Rossel Island) roughly equal in size to *N. vankampeni*. Kraus's report of these two new taxa is especially important because it provided the first phylogenetic analysis of all known species of *Nactus*. His analysis was based on a set of 23 morphological characters and yielded several hypotheses: (1) *N. galgajuga* (also the Mascarene *N. coindemirensis*) was not a member of the *Nactus pelagicus* clade; (2) the two other Australian *Nactus* (*cheverti*, *eboracensis*) were in the *pelagicus* clade, although they were not closely related to one another or other *Nactus*; (3) the three dwarf New Guinea *Nactus* were monophyletic; and (4) the southwest Pacific *Nactus* were a sister group to the Mascarene *N. serpensinsula*.

Jackman et al. (2008) performed the first phylogenetic analysis using nuclear and mitochondrial DNA for a small subset of *Nactus* species. Several relationship patterns were revealed and differed depending upon whether they derived from mtDNA or nuclear DNA or a combined data set. *Nactus pelagicus* (unisexual) and a southern PNG coast group member were sister groups with only the nuclear DNA sequences, although they were not closely related.

Subsequently, the Villanova laboratory (Heinicke et al., 2010) focused their phylogenetic analyses on a larger geographic and taxa sample of *Nactus*, as well as a larger molecular data set. These data and analyses were more revealing and more compatible with morphological appearance. The *pelagicus* group, as earlier delineated, was usually monotypic, and when it was not, Australian *N. eboracensis* and the southern coastal PNG sample were sisters and a sister group to *N. acutus*. A broad geographic sample of unisexual *N. pelagicus* was monotypic and always a sister group of *N. multicoloratus*. The two individuals of *N. multicoloratus* derived, one from the southern Solomon Islands (Santa Cruz Islands) and the other from central Vanuatu (Efate), were modestly but not strikingly distinct. The two widespread, although allopatric, Australian *Nactus* were not a sister pair; one was related to *N. galgajuga*, and the other was related to the southern PNG coast *Nactus*.

A more recent molecular phylogenetic analysis (Zug and Fisher, 2012) with an even broader geographic sampling of the *N. pelagicus* group suggests a broader (more inclusive) *pelagicus* group that includes all dwarf species. Their mitochondrial DNA phylogram closely matches the one in Heinicke et al. (2010). The nuclear DNA one does not, apparently owing to the additional samples. The major difference is the inclusion of the dwarf *Nactus* in a single clade that is distinctly different from the clade of the larger Australo-Papuan *Nactus* species. This larger clade contains two lineages: (1) a PNG south coast sample sister to the Australian *N. eboracensis* and (2) a predominantly north coast lineage that has a unisexual and bisexual "*pelagicus*" group of populations and a bisexual clade with the Australian *N. cheverti* and *N. galgajuga* sister to the Manus island *N. kunan*.

In 2009, Eckstut and colleagues compared seasonal variation in female reproduction of Vanuatu *N. multicoloratus* and *N. pelagicus*. Both appear to be primarily dry-season breeders, and evidence suggests that *N. pelagicus* deposits its eggs one to

two months earlier than *N. multicoloratus*. Neither species shows evidence of sperm storage in their oviducts. A subsequent study by Eckstut et al. (2013) examined the variability of chin scalation in these two species on Tanna Island, Vanuatu. The details of this study demonstrate a difference in the levels of variation. This variation is examined in the Morphology and Variation section.

Zug and Fisher (2012) described a boldly colored *Nactus* from Manus Island. This species was most closely related to the Australian clade of *N. galgajuga* and *N. cheverti*. This study, using DNA sequences from Heinicke's study and new ones from the north coast of PNG, demonstrated that the larger *Nactus* and the dwarf species represent a single clade, although they have distinct lineages. The results of our 2012 study are examined in more detail in the Geography, Relationships, and Taxonomy section.

MATERIALS AND METHODS

This study has had a long incubation. Formal data gathering of New Guinean specimens began in the late 1980s as a collaborative project with Brad Moon. Because two of us were gathering data, we developed a set of definitions for the recording morphology and tested our ability to measure and record each character in the same way. The initial character set was larger than the one reported herein because a few characters could not be recorded in a consistent manner or our preliminary analysis suggested some characters were redundant. A further refinement of the character set occurred during an examination of Australian *Nactus* (see comments in Zug, 1998).

When this study began, the *N. pelagicus* group was easy to define because only four sets of populations were recognized within the genus *Nactus*: (1) the Mascarene populations; (2) a single miniature New Guinean species, *N. vankampeni*; (3) a boldly banded Cape York species, *N. galgajuga*; and (4) a widespread southwest Pacific *N. pelagicus*. The latter had only recently been recognized as containing a broadly occurring unisexual population and several bisexual species. Because no taxonomic studies had yet been performed, *pelagicus* was applied to all, and by default, this group of cryptically brown-colored *Nactus* became the *pelagicus* complex or species group. This usage persists even though we now know it is a polyphyletic group (Heinicke et al., 2010; Zug and Fisher, 2012). Herein, I use "*Nactus pelagicus* complex" for all Pacific area *Nactus* populations with a mean SVL ≥ 42 mm that possess longitudinal rows of dorsal tubercles on the trunk.

The characters used herein are defined in Appendix A, Table A1. The various states and levels of variation are detailed in the Morphology and Variation section. The specimens examined are listed in Appendix B. The specimens represent 69 localities (Figure 1), totaling 854 individuals. My goal was to create small, geographically delimited samples of approximately 20 adults. There are 17 such samples or larger ones; another 13 samples contain between 10 and 19 individuals, and the remaining

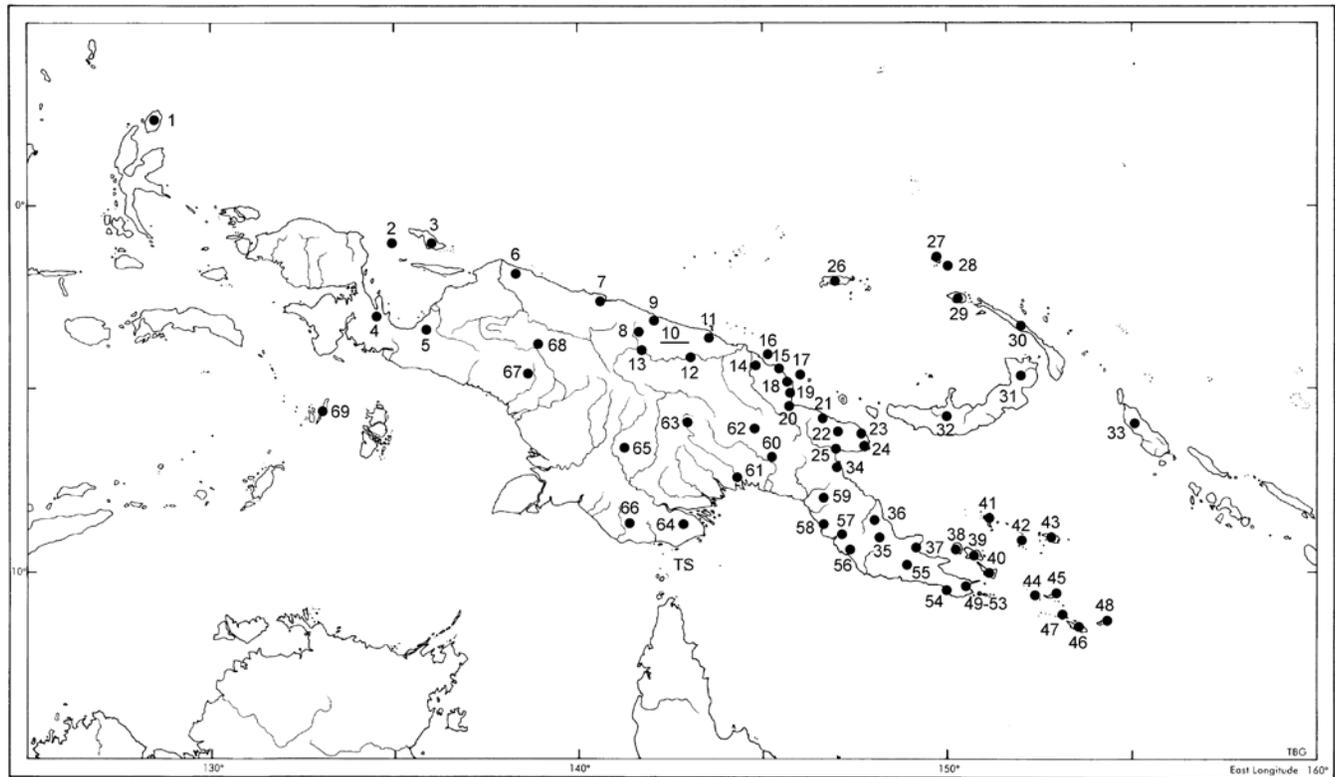


FIGURE 1. Map of New Guinea with sample localities. Distribution of samples within the New Guinea region. The numbers identify the sample localities. The locality names, sample sizes, and specimens in each sample are presented in Appendix B.

samples contain 9 or fewer individuals. In 17 samples, a locality is represented by only one or two individuals. These small samples are especially prevalent for Irian Jaya (Papua). Further, the number of sample localities (10 of the 66 samples) is lower for the western half of the island. I suspect this rarity reflects the bias of herpetological collectors and not the abundance of this gecko. Homogeneity, the presence of a single genetic entity, comprising a sample is another factor requiring consideration. Most locality samples have a high probability of representing the single genetic entity criteria. Most, however, is not all! Some samples are mixed or suspected to be of mixed composition. In those samples, I have attempted to create homogeneous subsamples, but I cannot be absolutely certain that I did. The potentially mixed samples are the northern PNG coast (samples 15, 16, 18, 22), Bougainville (32), and the Milne Bay lowland (49) through the Milne Bay southern mountains (54). The possible effect of mixing is presented in the Geography, Relationships, and Taxonomy section. Two genotypes have been identified in the Madang area (Donnellan and Moritz, 1995: fig. 3), one at a very low abundance because the one genotype was represented by a single specimen and vouchered (AMS R124051); this specimen was assigned to its own sample (19). Subsequently, another specimen was discovered and added to that sample. The Bougainville

sample contains representatives of both a unisexual population and a bisexual population; owing to the locality and date of collections difference, I believe that I have correctly segregated most female unisexual and bisexual individuals. The mainland Milne Bay samples comprise individuals collected over 50 years, and most of the early vouchers have imprecise locality data, making accurate sorting into restricted-locality samples difficult; however, the use of recently (post-1995) collected specimens with more precise collections data has allowed a more precise assignment to sample localities. The corrections are present in the text, Appendix Table A1, and Appendix B. For many of the recently collected Milne Bay specimens, I was able to recognize possible morphological differences and assigned those individuals to four different morphotypes (A–D). Please note that the sample sizes reported in the different tables (e.g., see Tables 3, 4, 5) may not match because different sets of characters can have different numbers of individuals with complete sets of characters in the different tables.

Statistical analyses were performed using Systat 12. I note that I present mean or average values for measurements because they are recorded as decimal values; in contrast, I report medians for scalation counts because scalation is recorded as integers and a fractional or decimal value does not exist in these data.

Coloration is absent from my data set. Although I am certain that there are consistent coloration (shades of brown and patterns of marks) differences among the populations (e.g., see fig. 2 of Heinicke et al., 2010), those data were not recorded because I could not develop a consistent coding at the beginning of the study.

The examined specimens came from many collections, which are abbreviated here for subsequent mention in the text.

AMNH	American Museum of Natural History
AMS	Australian Museum, Sydney
BMNH	The Natural History Museum, London
BPBM	Bernice P. Bishop Museum
BYU	Brigham Young University
CAS	California Academy of Sciences
FLMNH	Florida Museum of Natural History
FMNH	Field Museum of Natural History
IRSNB	Institut royal des Sciences naturelles de Belgique
LSUMZ	Louisiana State University Museum of Zoology
MCZ	Museum of Comparative Zoology, Harvard University
MNHN	Muséum national d'Histoire naturelle
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
PNGM	National Museum and Art Gallery, Port Moresby
RMNH	Nationaal Natuurhistorisch Museum (formerly Rijkmuseum van Natuurlijke Historie)
SAM	South Australian Museum
SMF	Natur-Museum und Forschungs-Institut Senckenberg
UF	Florida Museum of Natural History, University of Florida
UMMZ	University of Michigan Museum of Zoology
USNM	U.S. National Museum (National Museum of Natural History, Smithsonian Institution)
ZMA	Zoölogisch Museum, Universiteit van Amsterdam
ZMB	Museum für Naturkunde, Humboldt-Universität zu Berlin
ZSM	Zoologische Sammlung des Bayerischen Staates

MORPHOLOGY AND VARIATION

SEXUAL DIMORPHISM

Most previous studies of *Nactus* species have not examined dimorphism in and among populations and species. This absence results largely from limited sample size in geographically restricted samples or a focus on the all-female populations of *N. pelagicus*. I demonstrated (Zug, 1998) that dimorphism is variable among populations of the Australian *N. cheverti* and *N. eboracensis* and is typically confined to body size (SVL), excepting the usual presence of precloacal pores in males and their absence in females (but see below in this section). This

variation among populations might have resulted from small sample sizes and/or disproportionate differences in the number of females and males in the Australian samples. The following statistical examination of dimorphism in the New Guinean samples tests only samples that have at least 10 individuals of five or more females and five or more males or samples of 12 or more individuals with at least five individuals of one sex. Fifteen samples met those criteria. All characters ($n = 41$) except proportions were tested in each sample by Student's *t* tests without adjustments and were considered significant at $P = 0.05$ in the pooled variance portion of the analysis. Here and in subsequent examination of morphological variation, results are presented in a geographic clockwise manner as designated by numerical assignment of sample localities (see Appendix A; Figure 1).

The samples tested for dimorphism are number (#) 10 (Torricelli Mountains), 13 females/15 males; #15 (NW Madang), 9/12; #16 (Manam Island), 10/12; #17 (Karkar Island), 14/9; #18 (Alexishafen), 21/25; #31 (East New Britain), 16/11; #32 (West New Britain), 9/12; #39 (Fergusson Island), 10/10; #41 (Kiriwina), 13/11; #45 (Misima), 9/8; #51, 53 (Milne Bay D), 10/10; #56 (Central Province savanna), 12/20; #57 (Central Province forest), 12/15; #60 (gulf coast–Purari River), 24/6; and #66 (Western Province–Wipim), 8/6. Of these 15 samples, 8 possess one or more dimorphic mensural traits, and 7 display one or more dimorphic meristic traits (excluding precloacal pores) that are statistically significant ($P \leq 0.05$). Samples 10, 32, 39, 45, 57, and 66 have no dimorphic traits. Sample 15 has no mensural dimorphism; samples 16 and 17 have no meristic dimorphism. All other samples possess two or more dimorphic traits. The dimorphic traits are listed in Table 1 with their frequency of occurrence among the dimorphic samples.

Among the dimorphic traits, SVL, TrunkL, and SnW occur most frequently (Table 1), although they occur concurrently in the same samples only three times (samples 16 [Manam Island], 18 [Alexishafen], and 41 [Trobriand]). Among the meristic traits, few show significance, and only sample 31 (East New Britain) and sample 60 (gulf coast–Purari) have two or more dimorphic scalation traits. This low incidence of significance and the low concordance of dimorphic traits suggest the absence of dimorphism for most recorded traits, with the possible exception of SVL and TrunkL and sample 18 (Alexishafen) with eight traits (SVL, TrunkL, HeadL, HeadW, HeadH, NarEye, SnW, Inflab) being significant. Gulf coast–Purari (sample 17) has the next highest number with six dimorphic traits (HeadH, SnW, Postm, DorsTub, ForefLm, HindfLm).

Although I am equivocal on the presence of dimorphism for most traits and samples, the presence or absence of precloacal pores is unquestionably dimorphic in many samples. Among New Guinea samples and populations, precloacal pores are predominantly, but not exclusively, confined to males, predominantly in the sense that 50 of the 69 samples have no females with precloacal pores. Because a few of the samples (2, 62, 68) contain only one or two females and these females have pores and, conversely, larger samples (e.g., 26, 31) have many females but only one or

TABLE 1. Traits displaying dimorphism and their frequency of occurrence in the larger New Guinea *Nactus pelagicus* group samples ($n = 15$). Traits and their definitions are identified in the Appendix, Table A1.

Trait	Number of occurrences	Percent occurrence (%)
Metric traits		
SVL	4	27
TrunkL	5	33
SnForel	1	7
HeadL	3	20
HeadW	2	13
HeadH	2	13
NarEye	3	20
Interorb	1	7
SnW	4	27
Meristic traits		
Inflab	1	7
Postm	2	13
DorsTub	1	7
TubRow	2	13
TubHip	1	7
CloacS	1	7
CSTip	1	7
PreclPor	15	100
ForefLm	1	7
HindfLm	1	7

two of the females have pores, it is likely that the females-with-pores populations are greater than the 28% frequency displayed by my set of samples. A small adult sample ($n = 6$) from mainland Milne Bay (sample 51A) contains three adult females with well-developed precloacal pores. This sample is the only bisexual one with all females possessing pores and numerous pores (Table 2). Elsewhere, precloacal pores are absent in the unisexual Oceania *Nactus pelagicus* (Zug and Moon, 1995). In Vanuatu (Zug and Moon, 1995), *N. multicaudatus* males have pores; females do not. In Australia (Zug, 1998), most *N. cheverti* males have a few precloacal pores (median of three pores), and females lack precloacal pores. In most populations of the Australian *N. eboracensis*, most males possess precloacal pores (≥ 6), and in some populations, a few females have precloacal pores, although they have fewer pores than males. Only one male (IRSNB 15871.1384) in all the New Guinea samples ($n = 309$ adult males) displays two femoral pores. In Australia, only some males of *N. cheverti* have a few femoral pores, often on only one side.

Not all mature males bear precloacal pores (Table 2). Among the samples with some females with pores, there are only three samples in which males lack pores (sample nos. 11 [Wewak], 28 [Emirau], 42 [Egum]). These samples have few males, one to three, and I expect that if the samples were larger, some males would possess pores. The number of precloacal pores in males is variable among samples. Table 2 conveys most of the observed variation in precloacal pore number for the New Guinea males. For the total male sample ($n = 309$), the range is 0 to 15 pores, with a median of 8, and mean \pm standard deviation (SD) = 6.9 ± 3.89 . Twelve samples (11, 16, 17, 18, 20, 24, 28, 31, 42, 43, 56, 60) contain some males lacking pores. There is no geographic

TABLE 2. Distribution and frequency of precloacal pores in adult females and males in New Guinea *Nactus pelagicus* group samples. A dash (—) indicates no males in sample because population is all female.

Sample name and number	Sample size	Number of adult females	Number of females with pores (%)	Number of pores	
				Females	Males
Numfoor (2)	1	1	1 (100)	15	—
Wewak (11)	7	3	1 (33)	2	0
Madang, mountains (14)	4	2	1 (50)	6	7
Gusiko (23)	7	5	2 (40)	2–3	1
Manus, unisexual (26)	32	32	1 (3)	5	—
New Britain, West (32)	32	16	1 (6)	1	3–9
Bougainville, bisexual (33)	18	8	1 (13)	7	6–10
Misima (45)	19	8	7 (88)	1–6	4–7
Sudest/Tagula-U morph (46)	14	9	6 (67)	3–12	10–12
Milne Bay A (51)	6	3	3 (100)	6–12	12–14
Central Province, mountains (55)	13	4	2 (50)	7	7–8
Central Province, savanna (56)	37	12	1 (8)	1	0–7

(Continued)

TABLE 2. Continued.

Sample name and number	Sample size	Number of adult females	Number of females with pores (%)	Number of pores	
				Females	Males
Central Province, forest (57)	29	12	4 (33)	2–9	7–9
Gulf coast, Tekadu (59)	6	5	1 (20)	2	10
Gulf coast, Purari River (60)	32	25	16 (64)	4–11	0–12
Gulf coast, Kikori (61)	13	7	4 (57)	4–8	7–10
Highlands, Chimbu (62)	4	3	2 (67)	6–9	—
Western Province, Wipim (66)	15	8	6 (75)	4–12	9–15
Eilander River (68)	1	1	1 (100)	11	—

restriction of the latter condition, although 10 of the samples are north coast ones; however, north coast samples comprise roughly 75% of the samples. Even though not geographically focused, there appear to be two groups of samples, one group ($n = 33$) with a median of 9 or fewer pores and a second one ($n = 19$) with 10 or more pores. The ≥ 10 pore samples contain no males without pores; the ≤ 9 pore samples include all samples with some males lacking pores.

MEASUREMENTS

Body Size

Overall body size is reflected in three metrics (SVL, TrunkL, SnForel) and two proportions (TrunkL/SVL, SnForel/SVL; Table 3). Adult body size ranges from a minimum of 31.4 mm SVL (in samples 49, 50, 51C [Milne Bay C]) to a maximum of 82.1 mm SVL (sample 48 [Rossel-Yela W]) in all specimens examined. Sample body size averages range from 36.8 and 37.4 mm (nos. 19 [Alexishafen], 69 [Kei Island], respectively) to 76.7 mm (sample 46 [Sudest large]). Both of the samples with the smallest adults are single individual samples, and the largest-adults sample contains two individuals. In the significantly dimorphic samples, females on average are larger than males, with mean SVLs differing by ~2 to ~6 mm. Only in one sample (61 [Kikori]) are males larger, averaging 2.3 mm longer, but the sample size is small and the sexes are not significantly different. Most samples or localities (81%) have adults averaging 49 mm SVL or larger (Figure 2; Table 3), with the majority of the samples (65%) having mean SVLs between 49 and 60 mm. The three samples with specimens with minimum adult SVL are geographically distant (Kei, Alexishafen, and Milne Bay C). Alexishafen and Kei are samples of one individual each, and the Milne Bay sample ($n = 5$) has adults with 31.4–43.3 mm SVL. Sympatry of a large-individual population with a medium-sized one occurs also on the islands of Sudest (sample 47) and Rossel (sample 48), and these two size classes can be distinguished by scalation traits.

Examining average body size in a slightly more rigorous fashion, that is, restricting examination to samples with sample sizes ≥ 10 individuals ($n = 28$), yields a similar result, with means of < 50 mm SVL comprising 4% (only one sample), 50–59 mm comprising 68%, and ≥ 60 mm comprising 28% of samples (Table 3). The reliably small-bodied (< 50 mm mean SVL) sample is the Central Province savanna one (sample 55; mean = 43 mm, range = 37–48 mm SVL). The other small-bodied samples (3, 4, 5, 6, 8, 13, 19, 21, 37, 44, 49, 67, 69) may or may not represent the small-bodied population because their small sample size potentially skews their means (Table 3). At opposite end of the size range, large-bodied samples (≥ 60 mm SVL) are more numerous, and most have larger sample sizes, that is, > 10 individuals. These samples (#) occur in the eastern third of New Guinea, and many represent insular populations: New Britain (#31, 32), Bougainville bisexuals (#33), Kamiali (#34), Ferguson Island (#39), Misima (#45), Sudest midsize (#46), Rossel (#48), and Milne Bay A (#51). Smaller samples of potentially large-bodied populations are St. Matthias (#27, 28) and Sudest large (#46). All the remaining samples have mean SVL in the 50–59 mm range, and most of these samples each has a size range from the mid 40s to low 60s mm SVL. All the preceding data are summarized in Table 3.

Is there a geographic pattern in the distribution of body sizes? The samples with the smaller SVLs (means = 37–45 mm SVL) are widely scattered throughout the lowlands of New Guinea and, except for the Central Province savanna sample (56), derive from samples of one or a few individuals. Similarly, the insular *N. p. undulatus* (Kei Island) is a single individual (adult) sample, and that individual may or may not accurately reflect the size range of the Kei population. Most other insular samples have average SVLs of 50 mm or larger. The average sizes and ranges of the Central Province (56) sample are likely an accurate portrait of this population's mean and range. The segregation of the Central Province small-bodied individuals is also possible by scalation traits. The largest individuals are from the Louisiade Archipelago, but not all island groups in the Milne Bay area have populations of large individuals; most populations

TABLE 3. Select body size traits and their variation in adults of New Guinea *Nactus pelagicus* group samples. Values are for all adults unless one or more of the presented traits is sexually dimorphic; then both female and male values are presented. Snout–vent length (SVL) given as mean \pm standard deviation; range provided for $n > 1$; proportions given as median \pm SD and range. An asterisk (*) indicates a dimorphic state. TrunkL = trunk or body length; SnForel = snout to forelimb distance.

Sample number, name, size (n), and sex	SVL (mm)	TrunkL/SVL (%)	SnForel/SVL (%)
1. Morotai, 1♂	50.5	41	38
2. Numfoor, 1♀	51.8	47	39
3. Biak Island, 1♀	46.9	44	41
4. Yeretuar, 1♀	47.3	41	41
5. Nabire	44.4 \pm 2.40	40 \pm 2.0	40 \pm 2.0
2♂	42.7–46.1	39–42	39–41
6. Toem	46.2 \pm 2.94	43 \pm 1.9	38.5 \pm 2.1
6♀+♂	41.6–49.0	41–47	35–41
7. Jayapura, 1♂	53.7	38	44
8. Utai	48.4 \pm 1.41	41 \pm 4.1	43 \pm 0.8
2♀+♂	47.4–49.4	38–44	43–44
9. Aitape	50.4 \pm 1.56	40 \pm 3.1	43 \pm 0.8
2♀	49.3–51.5	37–42	43–44
10. Torricelli Mountains	53.1 \pm 4.19	41 \pm 2.9	41 \pm 1.8
28♀+♂	42.3–61.0	34–49	35–43
11. Wewak	52.7 \pm 5.07	38 \pm 7.7	45 \pm 3.2
7♀+♂	46.8–62.5	32–48	40–47
12. Sepik, Ambunti	51.0 \pm 3.36	42 \pm 2.5	40 \pm 1.0
13♀+♂	45–59	36–44	39–41
13. Sepik, Wagu	42.1 \pm 0.0	42 \pm 0.0	44 \pm 0.0
2♂	42.1	42	42
14. NW Madang, mountains	53.7 \pm 3.50	38.1 \pm 4.2	46 \pm 1.8
3♀+♂	50.9–57.6	35–44	44–47
15. Madang, coast	52.1 \pm 2.73	40 \pm 2.7	42 \pm 2.2
21♀+♂	47.0–56.5	35–45	37–46
16. Manam Island	57.6 \pm 4.49*	39 \pm 2.6*	42 \pm 1.4
10♀	49.6–64.3	36–44	40–43
12♂	53.5 \pm 3.06*	37 \pm 2.6*	45 \pm 2.8
	47.7–58.0	32–41	39–46
17. Karkar Island, 14♀	57.4 \pm 3.38*	40 \pm 2.9	41 \pm 2.1
	49.1–63.6	35–46	38–44
9♂	53.9 \pm 4.21*	39 \pm 3.2	41 \pm 4.2
	45.9–58.2	33–43	34–42
18. Alexishafen, 21♀	58.0 \pm 4.04*	40 \pm 2.8*	41 \pm 2.1
	48.3–63.6	35–46	36–44
25♂	52.2 \pm 4.76*	40 \pm 2.8*	41 \pm 1.9
	43.8–61.0	34–43	38–46
19. Alexishafen, 1♀	36.8	44	41
20. Madang	55.4 \pm 3.79	43 \pm 1.9	40 \pm 1.4
13♀+♂	51.0–61.3	38–44	38–42

(Continued)

TABLE 3. Continued.

Sample number, name, size (<i>n</i>), and sex	SVL (mm)	TrunkL/SVL (%)	SnForel/SVL (%)
21. Bom	48.7 ± 2.22	37 ± 2.8	42 ± 2.3
6♀+♂	46.9–52.8	33–40	39–46
22. Finisterre, 1♀	61.0	42	45
23. Guisko	50.1 ± 1.53	41 ± 3.1	39 ± 2.1
6♀+♂	48.0–51.5	36–45	35–40
24. Finschhafen	53.5 ± 4.49	38 ± 0.6	43 ± 2.8
5♀+♂	49.9–61.2	36–38	40–47
25. Lae	58.8 ± 4.36	42 ± 3.3	40 ± 1.1
7♀+♂	52.7–65.0	36–46	38–41
26. Manus Island	56.7 ± 2.90	38 ± 3.2	42 ± 2.1
21♀	49.1–61.1	32–42	37–46
27. St. Mathias, Mussau	64.4 ± 1.77	44 ± 6.4	40 ± 1.1
2♀	63.1–66.6	40–49	40–41
28. St. Matthias, Emirau	62.4 ± 7.87	38 ± 2.0	43 ± 1.3
4♀+♂	51.6–69.5	36–41	42–45
29. New Hanover	no vouchers	no vouchers	no vouchers
30. New Ireland	57.0 ± 4.73	39 ± 4.5	42 ± 1.6
24♀+♂	48.2–63.3	29–46	38–43
31. New Britain, East, 16♀	62.2 ± 3.52	41 ± 1.3*	40 ± 2.1
	56.5–67.1	39–43	36–43
11♂	60.0 ± 3.17	40 ± 2.5*	41 ± 1.5
	54.7–65.7	35–44	40–44
32. New Britain, West	59.8 ± 4.01	39 ± 2.5	39 ± 1.0
21♀+♂	52.5–67.2	35–44	38–41
33. Bougainville, bisexual	61.3 ± 5.77	41 ± 2.8	41 ± 2.3
18♀+♂	49.5–70.6	36–46	34–45
33. Bougainville, unisexual	57.0 ± 2.50	43 ± 2.8	41 ± 2.3
29♀	52.1–62.8	35–49	34–45
34. Morobe, Kamiali	67.9 ± 3.58	39 ± 2.7	43 ± 1.7
11♀+♂	61.5–73.1	35–45	41–45
35. Mount Lamington	64.2 ± 1.91	38 ± 2.0	41 ± 2.6
2♀+♂	62.8–65.5	37–40	39–42
36. Popondetta, 1♂	59.8	37	41
37. Collingwood Bay	47.8 ± 4.56	40 ± 1.2	41 ± 1.5
3♀+♂	44.5–53.0	39–41	40–43
38. Goodenough Island	58.1 ± 6.22	42 ± 3.5	39 ± 2.6
7♀+♂	45.1–61.9	37–47	37–44
39. Fergusson Island	63.3 ± 7.87	40 ± 2.0	40 ± 1.4
20♀+♂	46.6–74.1	37–46	37–42
40. Normandy Island	53.4 ± 5.31	40 ± 2.9	39 ± 1.5
13♀+♂	45.0–64.3	37–48	37–42
41. Kiriwina, 13♀	52.6 ± 3.77	40 ± 1.7*	40 ± 1.7
	43.1–56.9	38–44	38–44

TABLE 3. Continued.

Sample number, name, size (<i>n</i>), and sex	SVL (mm)	TrunkL/SVL (%)	SnForel/SVL (%)
11♂	49.1 ± 1.73 45.8–52.1	40 ± 1.9* 36–44	40 ± 1.6 38–43
42. Egum Atoll, Yanaba 2♀+♂	51.8 ± 0.50 51.4–52.1	39 ± 0.9 38–39	44 ± 1.8 42–45
43. Woodlark Island 3♀+♂	49.9 ± 3.47 47.1–53.8	40 ± 1.4 38–40	42 ± 2.1 40–44
44. Conflict Group 3♀+♂	47.5 ± 2.95 44.2–49.8	39 ± 2.5 38–42	37 ± 0.8 37–39
45. Misima 17♀+♂	66.9 ± 6.58 52.0–76.5	39 ± 2.2 33–42	41 ± 1.3 39–44
46. Sudest/Tagula, large species 2♀	76.7 ± 1.13 75.9–76.7	42 ± 3.0 39–44	41 ± 0.01 41–42
46. Sudest/Tagula, midsize species 15♀+♂	58.3 ± 5.82 38.7–61.9	42 ± 2.5 37–47	40 ± 1.8 37–43
47. Rossel-Nimowa 5♀	55.3 ± 4.21 50.0–61.0	43 ± 3.0 40–47	42 ± 1.6 39–43
48. Rossel-Yela U, 1♂	55.5	42	43
48. Rossel-Yela W 14♀+♂	61.2 ± 11.59 46.0–82.1	41 ± 2.8 37–45	43 ± 2.8 39–48
49. Alotau, lowlands 21♀+♂	53.6 ± 5.80 38.7–62.0	42 ± 2.3 37–47	40 ± 1.7 37–43
49, 51, 54A. 6♀+♂	66.5 ± 5.16 59.0–72.2	41 ± 2.3 38–43	41 ± 1.0 39–42
49, 50B. 7♀+♂	54.0 ± 5.74 42.8–49.1	41 ± 2.7 34–44	41 ± 1.2 39–43
49, 50, 51C. 5♀+♂	38.8 ± 4.50 31.4–43.3	42 ± 2.0 40–45	42 ± 2.4 39–44
51, 53D. 21♀+♂	62.0 ± 6.19 52.1–70.9	42 ± 2.1 37–45	41 ± 1.4 37–43
50. Alotau, East Cape Mountains 13♀+♂	59.9 ± 2.45 56.7–64.8	41 ± 2.5 33–45	41 ± 1.2 39–43
51. Milne Bay, Owen Stanley Range 14♀+♂	66.2 ± 12.4 31.4–72.2	41 ± 2.3 33–41	41 ± 1.1 40–44
52. Milne Bay, Sideia 3♀+♂	53.7 ± 5.50 48.3–59.3	39 ± 2.8 36–41	41 ± 2.2 39–43
53. Milne Bay, Fife Bay 20♀+♂	58.7 ± 5.46 50.0–67.3	42 ± 2.5 37–45	40 ± 1.6 37–43
54. Milne Bay, Southern Mountains 4♀+♂	59.7 ± 3.55 56–64	40 ± 3.1 36–43	41 ± 1.5 39–43
55. Central Province, eastern mountains 8♀+♂	52.3 ± 2.22 48.6–56.0	41 ± 1.5 39–43	43 ± 2.0 40–46
56. Central Province, savanna, 12♀	43.3 ± 3.17 38.5–47.1	44 ± 2.1 43–49	39 ± 2.1 36–43

(Continued)

TABLE 3. Continued.

Sample number, name, size (<i>n</i>), and sex	SVL (mm)	TrunkL/SVL (%)	SnForel/SVL (%)
21♂	42.0 ± 2.65 37.2–47.7	41 ± 2.8 33–46	39 ± 2.3 35–44
57. Central Province, forest 27♀+♂	57.4 ± 4.67 44.0–67.2	44 ± 3.5 35–49	39 ± 2.3 35–44
58. Central Province, Yule Island, 1♂	45.0	42	38
59. Gulf coast, Tekadu 5♀+♂	56.8 ± 4.40 51.0–61.4	45 ± 2.3 40–45	38 ± 4.2 37–47
60. Gulf coast, Purari River 30♀+♂	57.7 ± 4.04 49.1–64.4	43 ± 2.4 39–48	40 ± 2.9 31–46
61. Gulf coast, Kikori 12♀+♂	59.6 ± 3.27 53.8–64.0	41 ± 1.1 39–43	40 ± 1.9 39–45
62. Highlands, Chimbu 3♀	57.6 ± 4.63 52.5–61.5	43 ± 1.0 42–44	40 ± 0.6 39–40
63. Highlands, Waro 2♀+♂	55.8 ± 0.14 55.7–55.9	39 ± 0.2 38–39	42 ± 0.9 41–42
64. Western Province, Emeti 10♀+♂	51.4 ± 2.07 48.0–53.8	43 ± 3.0 36–46	40 ± 1.6 38–42
65. Western Province, south central	no adults		
66. Western Province, Wipim 14♀+♂	51.0 ± 3.36 45.0–58.1	41 ± 2.3 38–47	39 ± 2.0 36–44
67. Lorenz River, Sabang, 1♂	49.2	37	39
68. Eilander River, Wamena, 1♀	51.9	39	42
69. Kei Islands, 1♂	37.4	40	46

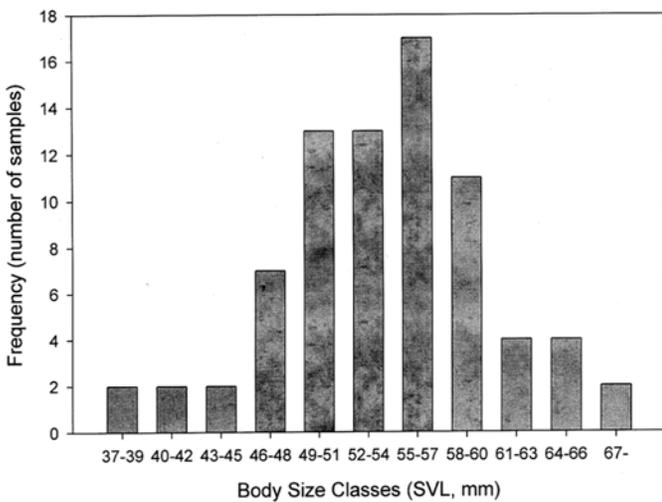


FIGURE 2. Frequency distribution (histogram) of average body size (SVL) for the combined New Guinea *Nactus pelagicus* group samples.

consist of midsize individuals (i.e., means of 50–60 mm SVL). In mainland samples, large size (means > 60 mm SVL) occurs only on the Morobe coast (samples 34, 35).

The pattern for body size proportions (TrunkL/SVL, SnForel/SVL) shows a high uniformity of shape with narrow ranges of 37%–47% and 38%–46%, respectively. The ranges become even narrower if a single outlier is removed from each group (i.e., 37%–43% and 38%–44%). These outliers derive from samples of one specimen each. This uniformity in shape precludes any geographic pattern.

Head Size and Shape

As would be predicted, the head metrics (Table 4) mimic the body metrics, with the longest individuals (>70 mm SVL) having the longest heads (HeadL > 19.0 mm). A strong association with SVL exists for all head measurements; Pearson correlation coefficients of head metrics to SVL ($n = 767$) range from 0.77 (Interorb) to 0.95 (HeadL). The constancy in body shape among all populational samples is highlighted by the narrow range of values for all head proportions (Figure 3): 25%–30%

TABLE 4. Select head size traits and their variation in adults of New Guinea *Nactus pelagicus* group samples. Values are for all adults unless noted otherwise. HeadL and HeadW are given as mean \pm standard deviation and range; proportions are given as median \pm SD and range. An asterisk (*) indicates a dimorphic state. HeadL = head length; HeadW = head width; NarEye = nares to orbit distance; SnW = snout width; SVL = snout-vent length.

Sample number, name, size (<i>n</i>), and sex	HeadL (mm)	HeadW (mm)	HeadL/SVL (%)	HeadW/SVL (%)	HeadW/HeadL (%)	NarEye/HeadL (%)	SnW/HeadL (%)
1. Morotai (<i>n</i> = 1♂)	13.8	8.8	27	17	64	30	16
2. Numfoor (1♀)	13.9	10.3	27	20	74	32	16
3. Biak Island (1♀)	13.2	8.7	28	19	66	30	13
4. Yeretuar (1♀)	12.7	8.0	27	17	63	34	14
5. Nabire	11.7 \pm 1.63	7.7 \pm 0.85	26 \pm 2.2	17 \pm 1.0	66 \pm 1.9	33 \pm 0.2	16 \pm 1.6
2♂	10.6–12.9	7.1–8.3	25–28	17–18	64–67	33–33	15–17
6. Toem	12.6 \pm 0.70	8.4 \pm 0.69	27 \pm 1.2	18 \pm 0.8	67 \pm 4.6	31 \pm 1.7	15 \pm 1.3
6♀+♂	11.5–13.5	7.2–9.3	25–29	17–19	62–75	29–33	14–17
7. Jayapura (1♂)	15.3	10.2	29	19	67	33	14
8. Utai	13.2 \pm 0.71	8.5 \pm 0.42	27 \pm 0.4	18 \pm 0.4	64 \pm 0.2	29 \pm 0.5	14 \pm 1.3
2♀+♂	12.7–13.7	8.2–8.8	27–28	17–18	64–65	28–29	13–15
9. Aitape	14.0 \pm 0.64	10.4 \pm 0.42	28 \pm 0.4	21 \pm 0.2	75 \pm 0.4	35 \pm 2.6	15 \pm 0.8
2♀	13.5–14.4	10.1–10.7	27–28	21–22	74–75	33–36	15–16
10. Torricelli Mountains	14.0 \pm 1.05	9.6 \pm 0.85	26 \pm 0.8	18 \pm 0.1	69 \pm 3.6	31 \pm 1.2	14 \pm 1.3
28♀+♂	11.3–15.9	7.9–10.8	25–29	16–20	60–74	29–35	10–16
11. Wewak	14.6 \pm 1.21	9.6 \pm 1.52	28 \pm 0.8	18 \pm 1.5	66 \pm 6.1	32 \pm 1.1	15 \pm 2.1
7♀+♂	13.1–16.7	8.3–12.5	27–29	16–20	58–75	31–34	13–20
12. Sepik, Ambunti	13.5 \pm 1.18	9.2 \pm 0.67	26 \pm 0.9	18 \pm 0.7	68 \pm 3.1	31 \pm 2.4	16 \pm 1.7
13♀+♂	12.2–16.5	8.0–10.4	25–28	17–19	62–73	27–34	14–19
13. Sepik, Wagu 2♂	11.7 \pm 0.0	8.1 \pm 0.0	28 \pm 0.0	19 \pm 0.0	69 \pm 0.0	31 \pm 0.0	15 \pm 0.0
14. NW Madang, mountains	15.1 \pm 1.06	10.4 \pm 0.57	28 \pm 0.3	20 \pm 1.2	70 \pm 5.1	32 \pm 1.3	13 \pm 0.7
3♀+♂	14.1–16.2	9.8–10.9	28–28	19–21	66–75	31–33	13–14
15. NW Madang, coast	14.4 \pm 1.15	10.0 \pm 1.10	28 \pm 1.5	19 \pm 1.6	70 \pm 5.8	32 \pm 1.7	14 \pm 1.4
21♀+♂	11.8–16.5	7.0–11.4	23–30	15–22	55–80	30–37	12–16.
16. Manam Island, 10♀	15.8 \pm 1.40	11.1 \pm 1.40	27 \pm 0.5	19 \pm 1.1	70 \pm 3.2	33 \pm 2.2	15 \pm 0.9*
	13.1–17.4	7.5–12.4	26–28	16–22	66–74	31–39	13–16
12♂	14.9 \pm 1.20	10.3 \pm 0.70	28 \pm 1.1	19 \pm 1.8	69 \pm 5.5	32 \pm 0.8	14 \pm 0.7*
	13.0–16.6	7.5–12.2	27–30	16–21	58–77	31–33	12–15
17. Karkar Island	15.4 \pm 1.16	10.2 \pm 0.78	28 \pm 1.5	18 \pm 1.5	66 \pm 3.7	33 \pm 2.5	14 \pm 1.0
23♀+♂	13.4–18.3	8.6–12.0	26–33	16–22	57–73	29–43	13–17
18. Alexishafen, 21♀	15.3 \pm 1.18	10.3 \pm 0.70	26 \pm 0.70	18 \pm 1.1	69 \pm 4.8	32 \pm 1.3	15 \pm 1.3
	12.5–16.8	8.9–11.8	25–28	16–20	59–75	29–34	12–17
25♂	14.3 \pm 1.57	9.2 \pm 0.66	27 \pm 1.4	18 \pm 1.3	66 \pm 5.7	32 \pm 1.3	14 \pm 1.4
	11.5–16.3	8.1–11.0	26–31	15.3–19.9	56–73	28–34	12–18
19. Alexishafen, unique (1♀)	9.2	7.0	25	19	76	34	16
20. Madang	15.5 \pm 1.79	10.1 \pm 0.87	27 \pm 3.6	18 \pm 0.9	66 \pm 5.9	29 \pm 3.6	14 \pm 1.7
13♀+♂	13.8–20.4	8.5–11.3	25–40	17–20	48–71	21–33	9–16
21. Bom	12.6 \pm 0.74	9.1 \pm 0.29	26 \pm 1.1	19 \pm 0.5	73 \pm 2.4	30.1 \pm 0.9	15 \pm 0.9
6♀+♂	11.7–13.8	8.8–9.6	24–27	18–20	70–77	29–32	13–16

(Continued)

TABLE 4. Continued.

Sample number, name, size (<i>n</i>), and sex	HeadL (mm)	HeadW (mm)	HeadL/ SVL (%)	HeadW/ SVL (%)	HeadW/ HeadL (%)	NarEye/ HeadL (%)	SnW/ HeadL (%)
22. Finisterre (1♂)	17.6	11.4	29	18	65	34	13
23. Guisko 6♀+♂	13.6 ± 0.8 13.4–13.8	8.8 ± 0.34 8.4–9.3	27.1 ± 0.1 26–28	18 ± 0.7 17–19	65 ± 2.1 63–68	29 ± 4.0 25–34	14 ± 0.6 13–15
24. Finschhafen 5♀+♂	15.0 ± 1.58 13.8–17.6	9.9 ± 0.91 9.1–11.4	28 ± 0.9 26–29	18 ± 0.6 18–19	66 ± 2.5 63–70	27 ± 0.6 26–29	14.4 ± 1.2 13–16
25. Lae 7♀+♂	15.7 ± 1.25 13.8–17.3	10.5 ± 0.97 9.5–11.8	27 ± 0.4 26–27	18 ± 0.7 17–19	68 ± 2.7 62–69	33 ± 1.0 31–33	17 ± 0.9 15–17
26. Manus Island, unisexual 22♀	15.3 ± 0.83 13.2–16.8	10.7 ± 0.97 8.5–12.0	27 ± 1.2 25–30	19 ± 1.6 16–21	70 ± 5.5 57–78	33 ± 1.0 31–35	15 ± 0.8 13–17
27. St. Mathias, Mussau 2♀	18.0 ± 0.78 17.4–18.5	12.3 ± 0.0 12.3	28 ± 2.0 27–29	19 ± 0.5 19–20	69 ± 3.0 67–71	34.0 ± 0.1 34–34	15.1 ± 0.7 15–16
28. St. Matthias, Emirau 4♀+♂	17.6 ± 1.50 15.6–19.2	11.5 ± 1.47 10.1–13.5	28 ± 1.7 26–30	19 ± 1.6 16–20	65 ± 3.6 62–70	32 ± 0.9 31–33	15.4 ± 0.9 15–17
30. New Ireland 24♀+♂	15.7 ± 1.16 13.4–17.8	10.5 ± 1.03 8.9–12.4	28 ± 1.1 26–31	18 ± 1.0 17–21	67 ± 3.4 60–75	33 ± 2.5 30–43	14 ± 1.5 11–18
31. New Britain, East 28♀+♂	16.6 ± 1.04 14.3–18.3	11.1 ± 1.11 9.0–13.6	27 ± 0.7 25–28	18 ± 1.1 16–21	67 ± 3.7 57–75	32 ± 0.7 31–34	14 ± 0.8 13–16
32. New Britain, West 17♀+♂	16.0 ± 1.14 14.2–19.4	10.4 ± 0.86 9.0–12.3	27 ± 0.8 25–29	17 ± 1.1 15–20	65 ± 3.8 56–71	32 ± 0.9 30–34	14 ± 1.2 11–15
33. Bougainville, bisexual 21♀+♂	18.1 ± 1.27 15.6–19.8	13.0 ± 1.85 10.8–17.0	28 ± 0.7 27–30	21 ± 4.1 17–29	67 ± 2.9 61–73	33 ± 1.9 30–36	15 ± 0.9 13–16
33. Bougainville, unisexual 26♀	15.2 ± 1.02 13.9–17.4	11.1 ± 1.64 9.1–11.3	27 ± 1.1 25–28	19 ± 0.7 18–28	70 ± 4.4 64–78	31 ± 0.7 30–32	14 ± 1.4 10–16
34. Morobe, Kamiali 11♀+♂	18.8 ± 0.85 17.2–20.1	12.5 ± 1.08 11.0–14.3	28 ± 0.7 27–29	18 ± 0.9 17–20	66 ± 3.5 61–71	33 ± 3.5 30–43	14 ± 1.1 13–16
35. Mount Lamington 2♀+♂	17.9 ± 0.0 17.9–17.9	12.3 ± 0.2 12.1–12.4	28 ± 0.2 27–29	19 ± 0.2 19–19	68 ± 1.2 68–69	33 ± 0.4 32–33	17 ± 1.6 16–18
36. Popondetta (1♂)	16.2	9.3	27	15	56	41	14
37. Collingwood Bay 3♀+♂	13.5 ± 1.37 12.6–16.1	9.1 ± 0.82 8.4–10.0	28 ± 0.8 28–29	19 ± 0.3 19–19	67 ± 2.9 65–71	33 ± 0.8 32–33	16 ± 2.1 13–17
38. Goodenough Island 7♀+	16.7 ± 3.2 11.5–22.0	10.3 ± 1.55 7.0–11.7	29 ± 4.7 26–39	18 ± 1.2 16–19	64 ± 6.9 47–68	28 ± 4.9 19–35	14 ± 2.0 10–15
39. Fergusson Island 20♀+♂	17.5 ± 2.05 13.2–20.4	11.3 ± 1.52 8.3–13.0	28 ± 0.8 26–30	18 ± 0.7 16–19	65 ± 2.6 58–68	33 ± 1.7 27–35	15 ± 0.9 13–17
40. Normandy Island 13♀+♂	14.3 ± 1.59 11.9–17.9	9.5 ± 1.10 8.1–11.9	27 ± 0.7 25–28	18 ± 0.6 17–19	67 ± 2.9 62–72	33 ± 1.1 31–34	15 ± 1.1 13–18
41. Kiriwina 24♀+♂	14.1 ± 0.93 12.2–15.9	9.3 ± 0.68 7.8–10.2	28 ± 0.7 26–29	18 ± 0.8 17–20	66 ± 2.5 61–70	31 ± 2.6 26–36	15 ± 1.2 12–17
42. Egum Atoll, Yanaba 2♀+♂	14.7 ± 0.85 14.1–15.3	8.6 ± 0.50 8.2–8.9	28 ± 1.4 27–29	17 ± 0.8 16–17	58 ± 0.0 58–58	33 ± 0.9 32–38	14 ± 1.1 14–15

TABLE 4. Continued.

Sample number, name, size (<i>n</i>), and sex	HeadL (mm)	HeadW (mm)	HeadL/ SVL (%)	HeadW/ SVL (%)	HeadW/ HeadL (%)	NarEye/ HeadL (%)	SnW/ HeadL (%)
43. Woodlark Island 3♀+♂	14.4 ± 1.16 13.6–15.7	8.9 ± 0.20 8.7–9.1	29 ± 0.5 29–29	18 ± 1.6 16–19	62 ± 6.1 55–67	33 ± 1.0 32–34	14 ± 0.3 13–14
44. Conflict Group 3♀+♂	12.9 ± 0.95 11.9–13.8	8.5 ± 0.67 7.7–8.9	27 ± 0.5 27–28	18 ± 0.5 17–18	66 ± 2.5 64–69	33 ± 1.0 32–34	16.0 ± 0.6 15–17
45. Misima 17♀+♂	19.2 ± 1.73 15.6–21.6	11.4 ± 1.37 8.3–13.6	29 ± 0.7 28–30	17 ± 1.0 15–18	60 ± 3.4 53–66	34 ± 1.2 32–36	14 ± 0.8 13–15
46. Sudest/Tagula-U 15♀+♂	15.9 ± 1.48 13.2–17.8	10.6 ± 0.70 8.9–11.6	27.8 ± 1.5 24–30	18 ± 0.5 17–19	67 ± 0.8 63–79	33 ± 0.16 31–36	14 ± 0.9 13–16
46. Sudest/Tagula-W 13♀+♂	17.1 ± 3.82 12.5–23.3	11.4 ± 2.44 7.9–15.6	28 ± 1.2 26–30	18 ± 0.5 17–18	69 ± 0.4 62–76	33 ± 0.1 30–34	14 ± 1.5 12–17
47. Rossel-Nimowa 5♀	14.8 ± 1.04 13.3–15.9	9.8 ± 0.77 8.8–10.5	27 ± 0.5 26–27	18 ± 0.5 17–18	66 ± 2.2 64–70	31 ± 0.9 29–31	14.1 ± 0.4 14–15
48. Rossel-Yela U (1♂)	16.0	9.8	29	18	61	31	13
48. Rossel-Yela W 13♀+♂	17.1 ± 3.68 12.5–23.3	11.4 ± 2.44 7.9–15.6	28 ± 1.2 26–30	18 ± 0.7 17–20	67 ± 3.6 62–76	32 ± 1.1 30–34	14 ± 1.5 12–17
49. Alotau, lowlands 21♀+♂	15.0 ± 2.06 9.9–22.0	9.6 ± 1.08 6.5–11.3	27 ± 2.5 25–39	17 ± 1.0 16–20	65 ± 4.4 47–71	33 ± 3.3 17–36	15 ± 1.3 10–16
49, 51, 54A. 6♀+♂	18.4 ± 1.28 16.3–19.6	11.8 ± 6.16 10.8–12.5	28 ± 0.6 27–28	18 ± 0.7 16–20	64 ± 0.2 61–66	33 ± 1.1 31–35	15 ± 0.4 14–15
49, 50B. 6♀+♂	14.7 ± 1.75 12.0–16.3	9.8 ± 1.42 7.9–11.3	28 ± 0.3 27–28	18 ± 0.9 17–20	67 ± 3.2 62–70	33 ± 0.5 33–34	15 ± 0.8 14–16
49, 50, 51C. 5♀+♂	10.5 ± 1.08 9.0–11.5	6.7 ± 0.50 6.0–7.5	27 ± 0.01 26–29	17 ± 1.0 16–19	64 ± 2.4 61–68	35 ± 6.6 30–43	16 ± 1.0 15–17
51, 53D. 21♀+♂	16.7 ± 1.69 13.7–19.1	10.6 ± 1.12 8.4–12.7	27 ± 0.5 26–28	17 ± 0.7 16–18	63 ± 2.1 58–67	32 ± 2.2 30–41	15 ± 1.1 13–17
50. Alotau, East Cape Mountains 4♀+♂	16.0 ± 0.29 15.7–16.3	10.5 ± 0.56 10.1–11.3	27 ± 0.7 26–27	18 ± 1.1 16–19	66 ± 2.8 63–69	34 ± 1.4 32–35	14 ± 1.2 13–15
51. Milne Bay, Owen Stanley Range 9♀+♂	16.2 ± 3.11 10.6–19.1	10.4 ± 2.17 6.5–12.5	27 ± 0.7 26–28	17 ± 0.7 16–18	64 ± 1.6 61–66	34 ± 3.7 31–43	15 ± 0.8 15–17
52. Milne Bay, Sideia 3♀+♂	14.6 ± 0.98 13.8–15.7	9.3 ± 0.97 8.2–10.1	27 ± 1.1 27–29	17 ± 0.5 17–18	63 ± 3.6 59–66	31 ± 2.8 28–33	14 ± 0.9 13–15
53. Milne Bay, Fife Bay 19♀+♂	15.7 ± 1.49 13.3–18.5	9.9 ± 0.86 8.4–11.7	27 ± 0.6 26–28	17 ± 0.7 16–18	63 ± 2.0 58–66	32 ± 2.4 29–41	15 ± 1.2 13–17
54. Milne Bay, Southern Mountains 15♀+♂	16.7 ± 3.0 9.0–19.6	10.7 ± 1.83 6.0–12.7	27 ± 0.7 26–29	17 ± 0.9 16–19	64 ± 2.5 59–68	32 ± 2.6 30–41	15 ± 0.8 14–17
55. Central Province, eastern mountains 8♀+♂	13.9 ± 0.62 13.2–14.9	9.7 ± 0.67 8.8–10.6	27 ± 0.7 25–27	19 ± 1.0 17–20	70 ± 4.6 65–79	31 ± 1.0 30–33	15 ± 0.8 14–16
56. Central Province, savanna 33♀+♂	11.1 ± 0.76 9.5–12.9	7.8 ± 0.68 6.4–9.4	26 ± 1.5 20–28	19 ± 1.5 14–21	71 ± 5.0 62–83	32 ± 1.9 28–36	16 ± 1.9 14–24
57. Central Province, forest 27♀+♂	15.2 ± 1.30 11.8–18.3	10.0 ± 0.87 7.7–11.9	26 ± 0.8 25–28	18 ± 0.9 16–19	66 ± 3.7 59–73	29. ± 2.7 25–35	14 ± 1.3 11–16

(Continued)

TABLE 4. Continued.

Sample number, name, size (<i>n</i>), and sex	HeadL (mm)	HeadW (mm)	HeadL/SVL (%)	HeadW/SVL (%)	HeadW/HeadL (%)	NarEye/HeadL (%)	SnW/HeadL (%)
58. Central Province, Yule Island, 1♂	11.2	8.4	25	19	75	28	16
59. Gulf coast, Tekadu 5♀+♂	15.3 ± 1.04 14.0–16.3	10.3 ± 0.74 9.3–11.3	26 ± 0.9 26–28	18 ± 1.1 17–20	68 ± 2.0 65–70	31 ± 1.4 29–33	14 ± 1.3 13–16
60. Gulf coast, Purari River, 24♀ 6♂	15.4 ± 0.98 13.0–17.0 15.8 ± 0.73 15.0–16.8	10.3 ± 0.62 8.8–11.3 10.8 ± 0.83 10.3–12.0	26 ± 1.2 25–29 28 ± 0.9 26–28	18 ± 1.0 16–20 19 ± 4.0 17–20	67 ± 2.6 61–72 68 ± 5.5 62–77	30 ± 2.0 27–35 31 ± 0.7 29–31	14 ± 1.2* 12–17 15 ± 0.9* 13–16
61. Gulf coast, Kikori 12♀+♂	15.9 ± 0.95 14.2–17.2	11.0 ± 1.01 9.6–12.7	27 ± 0.8 25–28	18 ± 1.3 17–21	68 ± 4.9 62–78	32 ± 1.4 30–35	15 ± 0.8 13–16
62. Highlands, Chimbu 3♀	15.5 ± 1.12 14.5–16.7	11.0 ± 1.53 9.7–12.7	27 ± 0.9 26–28	19 ± 1.4 18–21	70 ± 4.6 67–76	33 ± 1.1 31–33	14 ± 1.9 14–17
63. Highlands, Waro 2♀+♂	15.0 ± 0.0 15.0–15.0	9.3 ± 0.21 9.1–9.4	27 ± 0.1 27–27	17 ± 0.4 16–17	62 ± 1.4 61–63	33 ± 0 33–33	16 ± 0.8 15–16
64. Western Province, Emeti 10♀+♂	13.9 ± 0.99 12.4–15.8	9.2 ± 0.44 8.4–9.8	27 ± 1.4 25–30	18 ± 0.8 17–20	66 ± 3.4 60–72	28 ± 2.3 26–33	14 ± 1.1 12–15
65. Western Province, Lake Murray	no adult voucher	no adult voucher	no adult voucher	no adult voucher	no adult voucher	no adult voucher	no adult voucher
66. Western Province, southwest 14♀+♂	13.7 ± 0.81 12.2–15.0	9.2 ± 0.66 8.2–10.2	27 ± 0.6 26–28	18 ± 1.0 16–20	68 ± 2.7 63–72	33 ± 0.9 31–34	15 ± 0.7 15–17
67. Lorenz River, Sabang, 1♂	13.4	9.2	27	19	69	36	16
68. Eilander River, 1♀	13.6	9.0	26	17	66	31	15
69. Kei Islands, 1♂	11.3	7.3	30	20	65	29	12

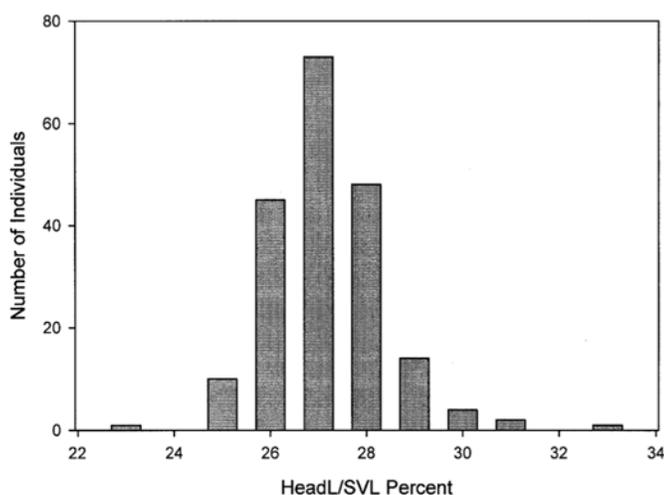


FIGURE 3. Frequency distribution of head size (HeadL/SVL percentages) in a sample ($n = 200$) from New Guinea *Nactus* populations.

(median of 27%) for HeadL/SVL, 17%–22% (18%) HeadW/SVL, 58%–75% (67%) HeadW/HeadL, 6%–8% (6%) EyeD/SVL, 21%–30% (24%) EyeD/HeadL, 27%–41% (32%–33%) NarEye/HeadL, 24%–34% (26%) Interorb/HL, and 12%–16% (14%) SnW/HeadL. The largest ranges in variation occur in HeadW/HeadL and NarEye/HeadL. Neither proportion displays sexual dimorphism in the testable samples (Table 1), and only HeadW as an individual trait has a relatively high occurrence of dimorphism. Aside from the difference in size already shown by SVL, there is no geographic pattern of variation among the head proportions. Indeed, I am struck by the high uniformity in all proportions among all samples (Tables 3, 4).

SCALATION

I quantified and recorded 19 features of scalation from the beginning of this study. These features include four from the head, three from the trunk, one from the tail, five from the limbs, and six from the circumcloacal and pelvic area. All 19 were recorded for all specimens examined if the trait was complete or undamaged. Other traits were identified subsequently by other

researchers, and these are reported only for a small subset of the individuals examined because they were identified or called to my attention after I had largely completed data gathering and museum visits. Some features of scalation are discussed in an earlier study (Zug and Fisher, 2012). Some of those observations are repeated below, although usually with an expanded description and discussion.

Head

In *Nactus*, as in many geckos, small granular and/or tuberculate scales cover most of the surface of the head. Larger, platelike scales form a border around the mouth (Figure 4). Above the mouth (upper lip) from front to rear, these scales are as follows: a large rectangular rostral is bordered posterior by variable-sized supranasals; supranasals are paired lunate scales, either in contact medially or slightly separated, allowing one (usually) or more granular head scales to touch the postero-medial edge of the rostral; each large naris is enclosed by a funneled nasal scale with only its rim on the exterior surface of the head; posteriorly, the nasal scale's rim is abutted by two or three postnasal scales, with the dorsalmost one being 2–3 times larger than the ventral two; and a series of supralabial scales border the mouth, large anteriorly, gradually shrinking posteriorly and beneath the rear of the eye, forming an upturned rictus (Figure 4). The lower jaw bears a large triangular to pentagonal mental scale forming the anterior edge of the mouth. Infralabials border the mouth, large anteriorly and shrinking beneath the eye to form a matching rictus with the supralabials; posteriorly, the mental is often bordered by a pair of variably sized postmental scales (Figure 5). If postmentals are absent, the granular chin scales contact the mental. This group of enlarged scales and their variation offer traits for differentiation.

My original character set did not include a rostral variable. As rostrals appear to vary, even if slightly, among populations, they may offer a trait for the differentiation of *Nactus*; however, no one has developed a standardized quantitative or qualitative measure to permit comparison of variation within and between samples and populations. This lament applies to other *Nactus* traits for which I offer descriptive comments but no statistical comparison among the populations. The rostral is a horizontal rectangular to parallelogram scale forming the tip of the snout. I note no proportional size differences (i.e., height to length) among the samples. All individuals have a posteromedial depression occupying the posterior half to two-thirds of the surface and a medial cleft extending from posterior to about the middle of the rostral. The cleft appears to be about the same proportional length in all individuals. The depression is somewhat more variable in the degree of concavity in different samples, but I am unable to express the differences quantitatively or qualitatively to yield a diagnostic trait.

A pair of supranasal scales abuts the posterior border of the rostral (Figure 4A). The possible diagnostic value of the shape and size of this pair and the presence or absence of small scales (inner nasals) separating them on the midline was proposed by Rösler

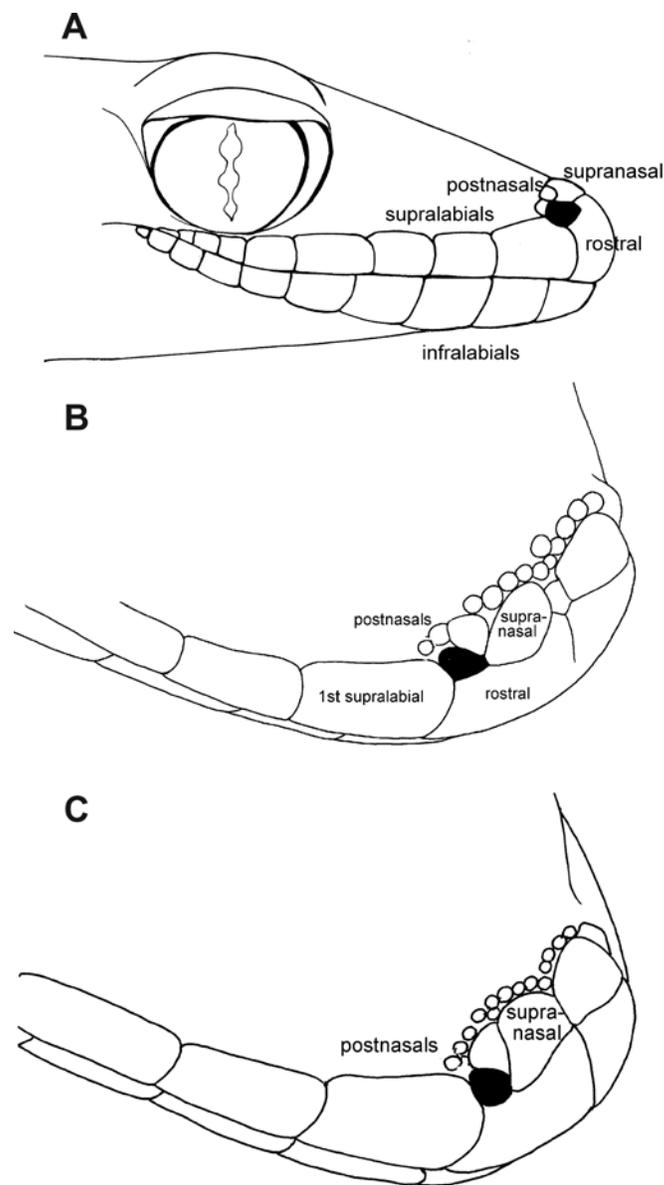


FIGURE 4. Head scale morphology in *Nactus pelagicus* complex geckos: (A) schematic lateral view of entire head highlighting two postnasal scales posteriorly abutting nasal scale containing the nares, (B) anterodorsal view of the snout with reduced supranasal scales separated by an enlarged granular scale and three postnasal scales abutting the nasal scale, and (C) anterodorsal view of the snout with slightly reduced supranasals separated only posteromedially and two postnasal scales abutting the nasal scale. (Illustration by M. D. Griffin.)

et al. (2005), although they provided no qualitative definition for recording differences and variation. Because I did not examine this trait until they identified it, I also provide a nonstatistical summary. The major features of the trait (Figure 4) are (1) supranasal square to rectangular (rounded corners posteriorly) and

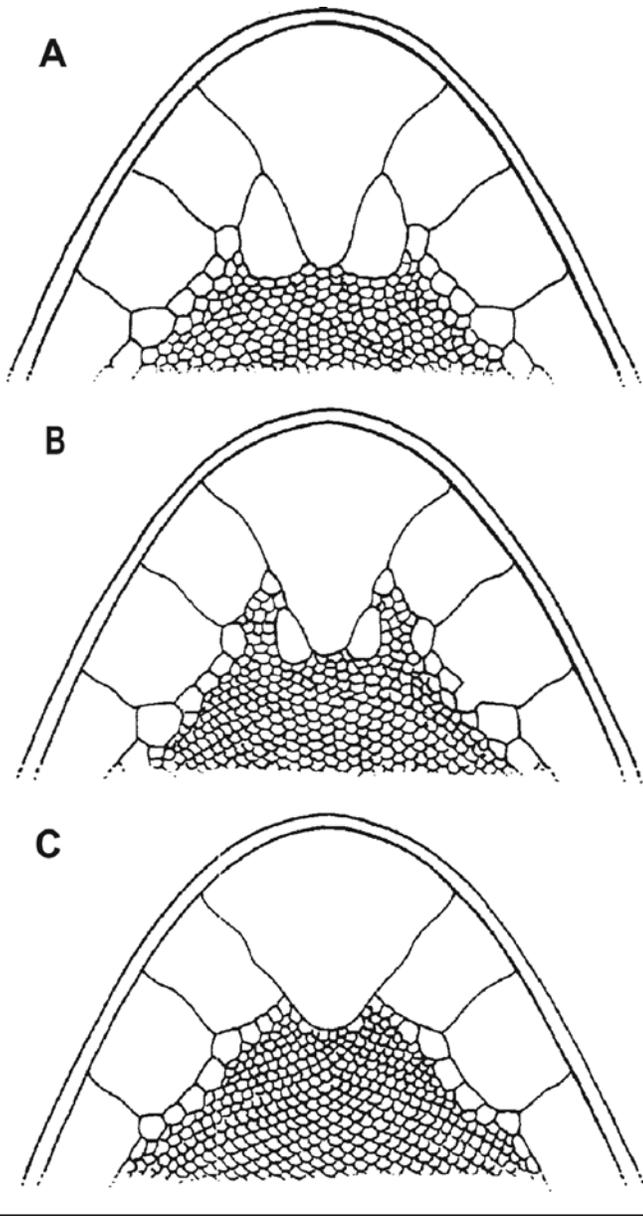


FIGURE 5. Schematic illustration of variation in the postmental scale morphology of New Guinea *Nactus* populations: (A) large postmentals excluding genials (chin scales) between the postmental and first infralabial, (B) moderately small postmentals with genials between the postmental and first infralabial, and (C) no postmentals, with genials contacting the posterior margin of the mental. Illustrations modified from Zug and Moon (1995: fig. 5).

left and right scales in full contact along the midline, (2) beginning of midline separation with supranasal becoming semilunate to flattened obovate but retaining midline contact at least anteriorly, and (3) full midline separation of supranasals and one (most frequent) or more granular scales (=internasals) touching

the posterior edge of the rostral (Figure 4B). The first feature or state occurs in all individuals of Karkar (sample #17), Admiralty (#26) unisexuales, Kamiali (#34), Kiriwina (#41), and Chimbu (#62). State 2 occurs commonly in samples with either state 1 (e.g., samples 6, 56, 57) or state 3; with my limited examination of state 3, it is not the exclusive condition in any of the larger samples. The reduced size of the supranasals occurs most commonly with state 3, for example, Bougainville bisexuales (#33) and Emeti (#64). Even with my limited data, the size and shape of supranasals and presence or absence of internasals appear to be too variable to serve as a diagnostic trait.

The nasal scale encompasses the nares and has little external expression other than a slight external border. I noted no variation in the shape and size of the nasal or naris; however, the number of postnasal scales contacting the posterior edge of the nasal is potentially diagnostic but, unfortunately, was not recorded for all samples. The postnasals number two or usually three scales (Figure 4); the dorsalmost one is always enlarged, typically circular, and in contact with the lateral edge of the supranasal, and the other two are equal in size to the adjacent granular scales of the head. The ventralmost one touches the first supralabial; it and the enlarged dorsal one are always present. The middle postnasal is the smallest one and typically has only a point contact with the nasal; if not in contact, it is not considered a postnasal scale. As for the supranasals and internasals, the number of postnasals (two vs. three) tends to vary within each sample.

The number of supralabial and infralabial scales (Suplab, Inflab) is, with rare exceptions, either three or four scales anterior to the front border of the exposed eye (Table 5). The three-Suplab state is more frequent (~60%) than four (~40%), two (~0.5%), or one (<0.5%) supralabials. For infralabials, three scales dominate (~75%) over four (23%), two (~2%), or one (~1%). There is no evidence of a geographic pattern in the variation of these scales, and because of the arbitrary use of the anterior edge of the lizard's eye and multiple years of data gathering, it is possible that I changed my perspective on what is the posteriormost scale, especially for the supralabials. The suture between the third and fourth infralabials regularly coincides with eye's anterior border, a much more regular feature than for the supralabials.

The mental scale has a variety of shapes (Figure 5), and potentially, this variation may affect its relative size. I did not attempt to quantify these differences, primarily because my preliminary investigation indicated that intrasample variation encompasses intersample variation. The size of the postmentals affects the shape of the mental by compressing its posterolateral borders, typically converting a triangular shape into a pentagonal one.

The paired postmental scales vary from large and totally filling the gap between the mental and the first supralabial on each side to absent (Figure 5; Table 5). To express this variation, I designed a measure of postmental scale size (Postm) to reflect the area that each postmental occupies relative to the number of nearby chin or genial scales (Zug, 1998). This metric successfully displays the size and variation within a population sample but is less successful in comparing relative size among samples.

TABLE 5. Select scalation traits and their variation in juveniles and adults of New Guinea *Nactus pelagicus* group samples. Values are for all specimens in each sample unless noted otherwise. The values are median and range. A dash (—) indicates that no count data were available; a question mark (?) indicates data are unclear. Suplab = supralabial scales; Postm = postmental scale size; PmLab = postmental-infralabial contact; DorsTub = rows of dorsal tubercles; TubRow = tubercles in a parasagittal tubercle row; PreclPor = precloacal pores; HindfLm = hindfoot lamellae; Subcaud = subcaudal scales.

Sample number, name, size (<i>n</i>), and sex	Suplab	Postm	PmLab	DorsTub	TubRow	PreclPor	HindfLm	Subcaud
1. Morotai	3.5	9	0	18.5	26	0	20.5	0
1♂, 1 juvenile	3–4	6–12	0	18–19	25–27	0	20–21	0
2. Numfoor, 1♀	3	12	0	15	34	15	20	0
3. Biak Island, 1♀	4	20	0	18	29	0	22	0
4. Yeretuar, 1♀	4	9	0	18.5	37	0	15	0
5. Nabire	3	8	1	15	34	10	20	0
2♂, 1 juvenile	3–3	6–8	0–1	14–15	33–38	10	20–22	0
6. Toem	3	10	0	14	35	0	21	0
7♀+♂, 1 juvenile	3–3	4–10	0	12–15	34–38	0	20–23	0
7. Jayapura, 1♂	3	8	1	17	38	11	21	0
8. Utai	4	16	0	14	35	0	22	0
2♀, 1 juvenile	4	12–18	0	13–15	30–40	0–9	21–23	0
9. Aitape	?	?	?	17	33.5	0	21	0
2♀, 2 juveniles	—	?	?	15–19	32–36	0–10	20–24	0
10. Torricelli Mountains	4	6	0	14	35	4.5	22	0
28♀+♂, 2 juveniles	3–4	0–16	0	13–16	30–40	0–10	19–26	0
11. Wewak	3	12	0	14	28	0	22	0
7♀+♂	3–4	6–14	0	13–17	24–36	0–2	20–24	0
12. Sepik, Ambunti	4	4	0	14	36	0	21	0
13♀+♂	3–4	2–18	0–1	12–16	33–39	0–10	20–24	0
13. Sepik, Wagu, 2♂	3 ± 0.0	6	0	14	35	9	22	0
14. NW Madang, mountains	3	16	0	19.5	32	6.5	22	0
4♀+♂	3	16–18	0	17–21	29–32	0–7	21–24	0
15. NW Madang, coast	3	16	0	18	28	2	21	0
22♀+♂	3–4	12–22	0	14–20	26–33	0–6	20–23	0–1
16. Manam Island	3	16	0	17	29.5	0	23	0
22♀+♂	3–4	12–22	0–1	14–19	26–35	0–4	20–26	0
17. Karkar Island	3	16	0	16	26	0	22	0
25♀+♂	3–4	12–22	0–1	13–18	23–30	0–8	20–24	0
18. Alexishafen	3	10	0	18	30	2	21	0
51♀+♂	3–4	0–22	0–2	15–21	22–37	0–12	19–25	0–1
19. Alexishafen, unique, 1♀	3	2	0	14	34	0	19	0
20. Madang	4	12	0	18	29	0	22	0
13♀+♂	3–4	2–22	0–3	16–22	22–34	0–3	19–24	0
21. Bom	3	10	0	14	29	0	19	0
13♀+♂	3	6–12	0–1	13–19	25–30	0–8	16–23	0
22. Finisterre, 1♂	4	16	0	13	26	12	22	1

(Continued)

TABLE 5. Continued.

Sample number, name, size (<i>n</i>), and sex	Suplab	Postm	PmLab	DorsTub	TubRow	PreclPor	HindfLm	Subcaud
23. Guisko	3.5	10	0	15.5	31	1	22.5	0
6♀+♂	3-4	8-20	0-1	12-18	28-35	0-3	22-23	0
24. Finschhafen	4	12	0	15	26	0	22	0
5♀+♂	3-4	8-14	0-1	14-16	23-29	0-2	21-23	0
25. Lae	4	10	0	14	29	0	20	1
7♀+♂	4	2-20	0-1	14-15	26-36	0-11	20-22	0-1
26. Manus Island, unisexual	4	10	0	15	32	0	25	0
32♀	3-5	8-18	0	12-19	28-37	0-5	21-26	0
27. St. Mathias, Mussau	3	0	—	17	30	0	22	1
3♀	3	0	—	17	29-31	0	21-25	0-1
28. St. Matthias, Emirau	3	13	0	15.5	35.5	0	22.5	0
6♀+♂	3-4	10-18	0	14-17	33-44	0	21-24	0
30. New Ireland	3	14	0.5	15.5	30	6	23	0
25♀+♂	3-4	2-22	0-2	14-17	27-41	0-12	19-24	0
31. New Britain, East	3	12	0	16	32	0	23	0
31♀+♂	3-4	2-24	0-2	15-19	27-37	0-9	20-25	0-1
32. New Britain, West	4	14	0	16	30.5	7	25	0
21♀+♂	3-4	6-22	0-1	15-18	24-35	0-10	23-25	0
33. Bougainville, bisexual	4	10	1	16	28.5	6.5	23.5	0
18♀+♂	3-4	6-14	0-3	12-18	23-35	0-10	20-25	0
33. Bougainville, unisexual	3	8	1	18	28	0	21	0
19♀	3-4	6-14	1-2	14-19	26-30	0	20-30	0
34. Morobe, Kamiali	4	8	0	19	30	0	22	0
12♀+♂	3-4	0-18	0-1	17-20	27-34	0-10	20-23	0-1
35. Mount Lamington	3.5	17.5	0.5	18.5	28.5	5.5	20.5	0
2♀+♂	3-4	16-19	0-1	18-19	27-30	0-11	20-21	0
36. Popondetta, 1♂	4	18	0	19	31	8	21	0
37. Collingwood Bay	4	14	0	17	28	0	22	0
3♀+♂	4	8-18	0	16-17	25-32	0-10	22-24	0
38. Goodenough Island	4	14	0	14	29	0	22	0
7♀+♂	3-4	10-20	0-2	14-17	25-40	0-13	19-24	0-1
39. Fergusson Island	4	14	0	16	31	0	22	0
21♀+♂	3-4	6-26	0-1	13-18	26-40	0-12	19-27	0
40. Normandy Island	3	10	0	18	27	0	21	0
16♀+♂	2-4	2-18	0-1	15-20	24-35	0-8	19-22	0
41. Kiriwina	4	10	0	16	29	0	22.5	0
24♀+♂	3-4	2-18	0-1	12-18	25-33	0-9	21-24	0
42. Egum Atoll, Yanaba	3	12	0	14	28	0	22	0
3♀+♂	3-4	10-14	0-1	13-14	26-29	0	21-23	0
43. Woodlark Island	4	14	0	15	30	0	21	0
3♀+♂	4-5	14-16	0-2	13-16	24-31	0-4	20-22	0
44. Conflict Group	3	14	0	15	26	7	21	0
3♀+♂	3	14-16	0-1	15-17	25-27	0-8	20-22	0

TABLE 5. Continued.

Sample number, name, size (<i>n</i>), and sex	Suplab	Postm	PmLab	DorsTub	TubRow	PreclPor	HindfLm	Subcaud
45. Misima	3	14	0	18	29	4	24	0
19♀+♂	3–4	8–22	0–1	16–19	22–33	0–7	21–26	0
46. Sudest-V	4	16	1	15.5	29.5	5.5	23	1
2♀	4	8–24	0–2	14–17	22–32	0–11	23	1
46. Sudest-U	3	24	0	18	27	10	21	0
15♀+♂	3–4	12–28	0	16–20	25–31	0–12	19–22	0
47. Rossel-Nimowa	3	26	0	20	29	0	20	0
5♀	3	24–28	0	17–21	26–31	0	20–21	0
48. Rossel-Yela U	3	20	0	18	28	0	21	0
15♀+♂	3–4	6–28	0–1	15–20	25–32	0–14	15–25	0–1
48. Rossel-Yela 1♂	3	26	0	18	30	11	27	0
49, 51, 54A.	4	14	0	16.5	29.5	12	22	0
6♂	3–4	10–20	0–1	15–18	28–34	6–14	19–23	0
49, 50B.	4	10	0	17.0	29	5	21	0
7♀+♂	3–4	6–18	0–1	13–18	26–31	0–9	19–23	0
49, 50, 51C.	3	16	1	13	30	0	22	1
7♀+♂	3–4	14–24	0–1	12–15	25–33	0–7	17–19	1
51, 53, 54D.	4	17	0	17	30	0	22	2
22♀+♂	3–5	12–24	0–1	14–19	25–33	0–15	18–24	2
49. Alotau, mixed	4	12	1	17	28	0	21	0
30♀+♂	3–4	6–20	0–2	13–18	24–34	0–9	18–23	0–1
50. Alotau, East Cape Mountains	4	14	0	17	28	6	21.5	0
4♀+♂	3–4	12–16	0–1	16–18	24–30	0–9	21–23	0
51. Milne Bay, Owen Stanley Range	4	17	0	15.5	30.5	0	21.5	1
12♀+♂	3–4	10–24	0–1	12–17	25–34	0–14	17–23	0–2
52. Milne Bay, Sideia	3	20	0	16	25	0	22	0
3♀+♂	3–4	16–22	0	14–17	24–26	0–7	22–24	0
53. Milne Bay, Fife Bay	4	16	0	18	31	11	23	0
17♀+♂	3–4	14–20	0–1	16–18	26–34	0–13	22–23	0–1
54. Milne Bay C	3	18	1	13.5	31	0	18	1
4♀	3–4	14–24	0–1	12–14	30–33	0–0	17–19	1
55. Central Province, eastern mountains	3	16	0	14	28	5	20	0
13♀+♂	3–4	10–22	0–1	13–16	24–33	0–8	17–22	0
56, 58. Central Province, savanna	3	12	0	13	24	3	18	0
36♀+♂	3–4	6–20	0	11–14	19–32	0–7	16–20	0
57. Central Province, forest	3	16	0	15	28	7	22	0
29♀+♂	3–4	10–22	0–1	13–17	21–31	0–9	19–24	0
59. Gulf coast, Tekadu	3	12	0	15	35	0	20	0
5♀+♂	3	6–18	0	14–17	26–37	0–10	19–20	0
60. Gulf coast, Purari River	3	10	0	14	33	6	23	0
33♀+♂	3–4	0–18	0–4	12–17	28–41	0–12	19–25	0
61. Gulf coast, Kikori	3	0	—	14	32	7	21	0
12♀+♂	2–3	0	—	11–17	23–34	0–10	20–22	0

(Continued)

TABLE 5. Continued.

Sample number, name, size (<i>n</i>), and sex	Suplab	Postm	PmLab	DorsTub	TubRow	PreclPor	HindfLm	Subcaud
62. Highlands, Chimbu 4♀+♂	3 3–4	8 6–10	0 0–1	14 14	28.5 27–30	3 0–9	22 20–23	0 0
63. Highlands, Waro 2♀+♂	3 3	14 12–16	0 0	13.5 13–14	28 26–30	6 0–12	22.5 22–23	0 0
64. Western Province, Emeti 10♀+♂	3.5 3–4	0 0–10	0 0	13 12–15	35 31–37	7.5 0–14	21 18–22	0 0
65. Western Province, Lake Murray	3	2	1	13	36	0	19	0
66. Western Province, southwest 16♀+♂	3 3	0 0–8	0 0	12.5 11–14	35 24–40	10 0–15	20 19–21	0 0
67. Lorenz River, Sabang, 1♂	—	—	—	12	37	11	20	0
68. Eilander River, 1♀	3	4	0	16	39	11	22	0
69. Kei Islands, 1♂	5	0	0	12	40	10	17	0

The latter difficulty arises from the difference in the size of the genials, which are clearly smaller in some populations than in other ones but not quantified. Thus, an average Postm of 16 for one sample versus 16 for another sample typically indicates comparably sized postmentals; however, equality might not always be exact because of differently sized genial scales among the different samples. PmLab assists in the interpretation of relative size. For example, if two populations share a PmLab of 0, that is, no genials between the postmental and abutting first infralabial scale, then a value of 16 indicates that postmentals are of equal size; however if PmLab is 0 for one sample and 1 or 2 for another, then the former sample likely has a larger postmental, if only slightly, than the latter sample even if Postm = 16 in both. Both characters are essential for recognizing the general appearance of the chin scalation. Eckstut et al. (2013) developed a seven-class system to score postmental size for evaluating variation in samples of *Nactus pelagicus* on a single island (Tanna Island, Vanuatu). Their results are discussed in the Geography, Relationships, and Taxonomy section. The preceding area values and all subsequent counts are median values. Because counts are integer values, I believe that the median is of more value than a fractional mean when describing unitary characters.

Postm and PmLab show moderate intrasample variation. Postmentals are present in most samples of New Guinea *Nactus* (Table 5) but not invariably so. Only a single sample (#62, Fly River) has a majority of individuals without postmentals. Because this a moderate-sized sample ($n = 12$), the total absence of Postm is a likely characteristic of this population. The St. Mathias–Musau sample (27) might also totally lack Postm; however, its sample size ($n = 3$) is too small to reliably conclude the absence in the entire population. This uncertainty is reinforced by some larger samples (e.g., East Sepik, Morobe-Kamiali, gulf coast–Purari)

having one or a few individuals lacking postmentals. Is this intrapopulation variation or a mixed sample? Examining the SD of postmental size in the larger ($n \geq 20$) samples offers a possible answer. Thirteen samples (10, 14–18, 30–32, 41, 49D, 54, 60) meet the larger-size criterion. Their SDs range from 2.14 to 5.46. Of these samples, three (10, 18, 60) have individuals lacking postmentals and SDs of 3.90, 5.20, and 3.68, respectively, suggesting that the absence of few individuals without a postmental is within the normal range of variation for populations.

Where samples are large and postmental size varies from small or absent to extremely large (e.g., sample 18, East Sepik, $n = 51$), the presence of two species in a sample requires consideration. Using the area measurement of 10 to 12 as the dividing line between large and small postmentals (see Table 5, median values), populations with large postmentals occur on the north coast of New Guinea in the Madang area (samples 14, 17). Most samples from the eastern islands (samples 42–48) also have large postmentals, with those of the Rossel group having the largest median size. Large postmentals are also the condition for most mainland Milne Bay samples and westward along the south coast to eastern Gulf Province. In the Western Province, the median condition is the absence of postmentals.

PmLab, postmental-infralabial contact, indicates whether the postmental contacts the ventral or medial edge of the first infralabial and is measured by the number chin scales lying in a perpendicular line between the latter two scales. Typically, one would expect a high association of the presence of PmLab of 1 or higher; that is, when a postmental is small, space is available for a genial scale to wedge itself between the two large scales. Yet the association between small postmentals and PmLab of 1 or higher is not as strong as expected. Of the 773 specimens with Postm and PmLab data, for a PmLab of 1 or 2, 6.4% have Postm of 6 or less, 3.4%

have Postm of 8, 3.1% have Postm of 10, but 8.3% have Postm of ≥ 12 . (Postm size is recorded only in even numbers.)

There appears to be a geographic association with Postm of ≥ 8 . I assume this association reflects a difference in shape of the postmental, specifically a narrowing of the Postm along its longitudinal axis. The New Ireland sample (30, $n = 25$) has a median Postm of 14 with only one individual with Postm < 8 . The Milne Bay D sample ($n = 21$) has a large (12–24 range) Postm, with half of the sample having PmLab of 1. The other Milne Bay samples (50–54) also have a large Postm, and many individuals have PmLab of 1.

Body and Limbs

Is there a similar association between the number of longitudinal rows of tubercles at the midbody (DorsTub) and the number of tubercles in a parasagittal row of dorsal tubercles (TubRow)? Using samples of five or more individuals, there is an association (Figure 6; the regression equation is $\text{TubRow} = 37.788 - 0.480 \text{ DorsTub}$) but not a strong correlation ($r = -0.31$, $n = 44$). The majority of the samples cluster between 28 and 32 DorsTub and 14 and 15 TubRow, with two outlier clusters. The low-DorsTub clusters consist of two samples of 13 TubRow, one with a median of 24 DorsTub and another with a median of 26 DorsTub. The localities of these two cluster are geographically distant, Wewak (sample 11) and Goodenough Island (sample 38). The high-DorsTub value cluster (≥ 35 , with 13–15.5 TubRow) has eight members (samples 6, 10, 12, 28, 54, 59, 64, 66) and is also geographically widespread, occurring on both the north

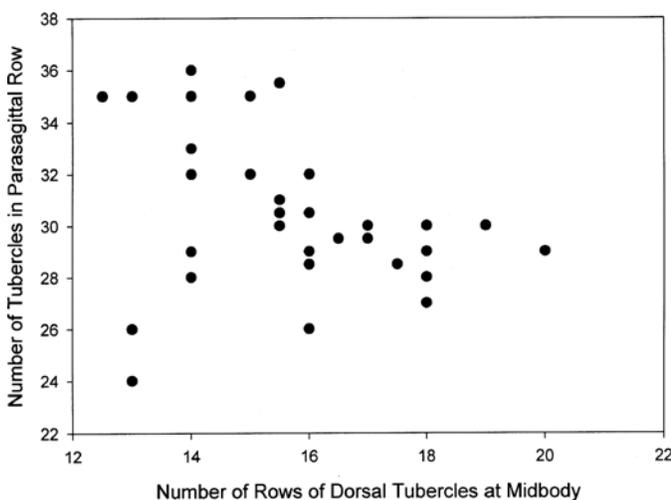


FIGURE 6. Association of the number (median) of dorsal tubercle rows (DorsTub; median) and number of tubercles in a parasagittal row of tubercles (TubRow; median) in select samples ($n \geq 5$ individuals per sample) of New Guinea *Nactus pelagicus* group members.

(Toem to Milne Bay) and south (Tekadu to Western Province) coasts. Although sample size may influence the median value, the high- and low-value groups are real and reflect regional differentiation and possibly adaptation to predators, substrate, or other environmental features.

Three other tubercle traits were examined: TubHip, TubHindl, and TubDens. The first trait concerns the number of tubercle rows across the sacrum. The range over all samples is 6 to 11, with a median of 9 tubercle rows, but with $\sim 45\%$ of the individuals with 10 rows, $\sim 35\%$ with 8 rows, and $\sim 20\%$ with 9 rows. No geographic pattern is evident, although at any location (sample site) 8, 9, or 10 rows dominate.

The presence or absence of enlarged tubercles on the dorsal surface of the hindlimbs (TubHindl) was coded as three states: (0) none, (1) on only the crus, and (2) on both the thigh and crus (Figure 7). This coding of tubercle occurrence is adequate but simplistic because it ignores the density and distribution on the limb surface (Figure 8). I attempted to record these aspects by using a density trait (TubDens) with three states from sparse to numerous and close. TubDens assists in identifying and coding the appearance of the limb surface but still is inadequate in differentiating the variety of surface morphologies observed.

Twenty-two samples (4–8, 12–13, 22, 25, 46V, 49C, 51C, 54C, 59, 62–69) have individuals lacking tubercles on the hindlimb. Of these samples, seven also contain a few individuals with tubercles only on the crus (#46V, 55, 59) or tubercles on the crus and thigh (#10, 19, 60, 61). No samples are characterized by tubercles only on the thigh. In those samples

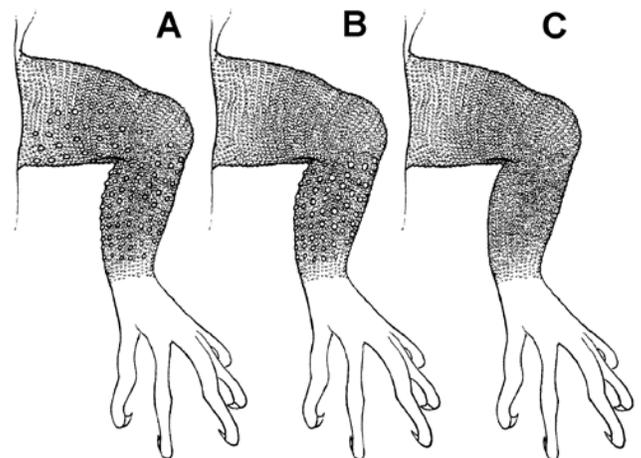


FIGURE 7. Schematic representation of tubercle traits of the hindlimbs of New Guinea *Nactus pelagicus* group members: (A) no tubercles present, (B) tubercles present on only the thigh, and (C) tubercles present on the thigh and crus. Illustrations modified from Zug (1998: fig. 3).

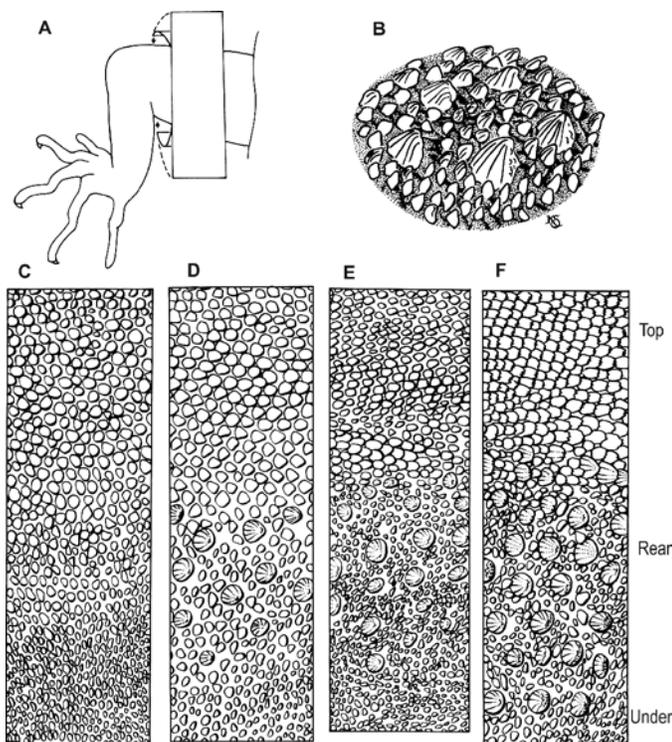


FIGURE 8. Variation in hindlimb enlarged tubercle distribution and density: (A) schematic hindlimb, with the rectangle depicting the location of skin stripes illustrated in C–F, (B) schematic close-up of a patch of hindlimb tubercles, (C) hindlimb lacking enlarged tubercles, (D) few enlarged tubercles on the posterior surface of hindlimb, (E) modest number of enlarged tubercles on the posterior surface, and (F) numerous enlarged tubercles on the rear surface. Also note the difference in size and density of the tubercles on the upper or dorsal surface of the hindlimb. (Illustrated by K. Spencer.)

containing “crus-only” individuals (#14, 15, 18, 21, 42, 46V, 42, 54–56), some also have individuals with tubercles on both the thigh and crus (#15, 18, 42). No sample possesses all three TubHindl states. The most frequent condition is tubercles on the crus and thigh and occurs in about 75% of the samples (1–3, 9–11, 15–20, 23–24, 26–45, 46U, 47, 48W, 49, 51A, 51D, 53, 53D, 54A, 54D, 55, 57, 60–61). I interpret a sample with a TubHindl single state as having all individuals drawn from a genetically similar population or group of populations and a sample with multiple states as potentially being drawn from two or more genetically distinct populations. The Torricelli Mountains sample (#10, $n = 30$) likely represents the latter situation as I created this regional sample by combining individuals from five localities along or adjacent to the Torricelli mountain range. Other samples with mixed states are less easily deciphered. For example, the Manam Island sample (#11) has

individuals with no hindlimb tubercles and with tubercles on both upper and lower limb segments. The former are all from the IRSNB collection; the latter are from AMNH. These data were obviously collected at different times. Did my visual concept of the two states change? Or are there two morphotypes in different localities within the Manam Island complex? In other samples, such as the Central Province savanna sample (#56), the majority of individuals showed state 2, and a few showed state 1. Was this a recording error or developmental variation within a single genetic population? I have no single or unequivocal answer for the preceding variation and will address the matter in the Geography, Relationships, and Taxonomy section.

As noted in the Materials and Methods section, TubDens is an attempt to account for the different tuberculate surface morphologies of the hindlimb. Although it was recorded for all specimens as a numerically coded character, it does not adequately describe the multiple conditions observed (e.g., Figure 8). I have decided that a summary here is unnecessary and would not accurately encompass the diversity in New Guinea *Nactus*. Because I think that this limb surface morphology differentiates populations, I will examine the regional geographic variation in detail in the Geography, Relationships, and Taxonomy section.

Initially, the number of cloacal spurs (CloacS) and the shape or degree of smoothness of the outer edge (CSTip) seemed to have some regional variation. With more samples and wider geographic sampling, their importance seems less robust. One (~43%) and two (~56%) cloacal spurs are predominant states in the total sample of New Guinea *Nactus* (as a reminder, the number refers to the number of spurs on only the right side; symmetry is the usual state). The percentages are nearly equivalent for the total adult female and the total adult male samples. No (<1%) and three (~1%) spurs occur in the remainder of the total sample with no evidence of dimorphism. Geographically, there is a preponderance of a single cloacal spur in the northern PNG samples from Maraup (#14) through Mydras Plantation (#20). Thereafter, the localities (#21–33) have a subequal mix of one and two spurs. Interestingly, the Manus unisexual sample (#26) has nearly equal numbers of one- and two-spurred individuals, in contrast to the Bougainville unisexual sample (#33) with only a single spur. The bisexual Bougainville sample (#33) has nearly equal numbers of one- and two-spurred individuals. On the north coast at Kamiali (#34), two spurs become the predominate state and remain the major state for all the remaining samples (#34–69).

The tip or outer edge of the cloacal spurs (CSTip) has two states: blunt or rounded edge, although not necessarily smooth, and peaked or pointed. Round-edged spurs are the dominant condition (68% of total sample), and pointed spurs are less common (32%) in the total *Nactus* sample. Because most large samples have a mix of two states, I find no geographic pattern with the exception of the southern PNG coast samples (#55–60) that have predominantly pointed spurs.

The presence or absence of secreting preloacal and/or femoral pores is often considered a sexually dimorphic feature

of geckos, with males having secreting pores and females lacking them. That generality has proved not to be the situation in the *Nactus pelagicus* group (see Zug, 1998), and New Guinea members show considerable variation in and among samples. I recorded four characters (PreclPor, FemPor, PoreC, TotPore [total number of pores; i.e., sum of PreclPor and FemPor]). Three of these traits can be quickly summarized. Femoral pores (FemPor) occurred in only two samples (21, 45) and only in one individual each in the two samples; in sample 45, the femoral pores occur in a female. Where present, there was no contact between the femoral and preloacal pore series. Because femoral pores were a rarity, TotPore equals the total number of preloacal pores. Hence, the following discussion concerns only preloacal pores.

Most samples possessed females without pores, but there are exceptions (Table 2). Nineteen samples include adult females with pores, and these samples are geographically widespread, occurring throughout the entire New Guinea distribution of the *N. pelagicus* group. Excluding female samples of one to three individuals, most samples have less than half of the females with pores. However, eight samples have more than half of the adult females with pores (Table 2), and these samples have two geographic foci, the Louisiade Archipelago (samples 45, 46) and Papuan Gulf coast (samples 60, 61, 62, 66). In the Louisiade females with pores, the maximum number of pores equals the maximum number in males; however, some females have distinctly fewer pores than males. A similar, but less robust, pattern exists for gulf females.

As noted in the sexual dimorphism results, the presence of preloacal pores is the usual condition for adult males but not a universal state; that is, 12 samples have one or more males lacking pores. In none of these latter samples is the absence of pores the majority condition. Repeating the Sexual Dimorphism section's observations, there are two groups of males: (1) those with 9 or fewer pores and the occasional male lacking pores and (2) samples with males having 10 or more pores and no males lacking pores. No strong geographic focus is observed, although the samples containing males without pores were north coast samples.

Three traits examine variation in subdigital lamellae (ForefLm, HindfLm) and the number of scales on the palm (Palm). The median number of forefoot lamellae varies from 13 to 22 for all *Nactus* samples. The most frequent median is 18 lamellae (33% of total samples), with 16 (21%) and 17 (17%) being the next dominant states. These three states account for the majority (71%) of the samples. In the larger samples ($n \geq 10$), there is no geographic locus for ForefLm. A similar absence of a geographic locus also is the condition for hindfoot lamellae. The median number of HindfLm ranges from 19 to 23 for all samples (Table 5). The total range of HindfLm is 15–30, but the range of medians is much narrower. The median is 22 in 35% of samples and 21 in 22%, and it rapidly tails off to 20 (13%) and 23 (10%). The number of Palm scales varies from 4 to 9, with medians of 5 (47%), 6 (38%), and 7 (10%) being the principal variants. Again, there are no geographic loci for any of the medians.

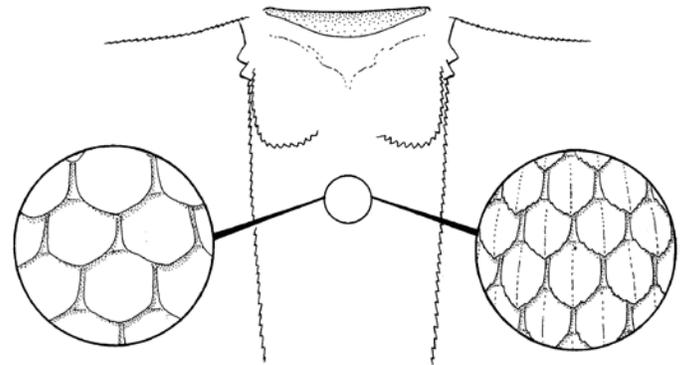


FIGURE 9. Schematic illustration of the underside of a *Nactus* tail with a depiction of smooth subcaudal scales on the left and keeled subcaudal scales on the right. Illustrations are from Zug (1998: fig. 2).

Keeled subcaudal scales (Figure 9) are the dominant condition for most New Guinea samples, exclusively so for 55 samples. Smooth subcaudals occur as an infrequent (<20% of a sample; $n \geq 10$ individuals) variant in samples 15, 18, 31, 34, 38, and 54. In smaller samples with $n < 10$, smooth subcaudals occur in samples 22, 25, 27, 38, 46V, 49C, and 53, and this condition is the “major” subcaudal state, such as in subsample 49C, in which all individuals ($n = 7$) possess smooth subcaudals. Another character state (smooth subcaudals at the base and keeled for most of an unregenerated tail's length) occurs exclusively in subsample 49D ($n = 22$). Geographically, smooth subcaudals occur only in north coast populations and are the dominant state in samples from localities #25, 27, and 49C. Mainland Milne Bay samples display a variety of states.

GEOGRAPHY, RELATIONSHIPS, AND TAXONOMY

GENETIC LINEAGES

Genetic sampling is still too sparse to provide a satisfactory resolution to interrelationships among the New Guinea *pelagicus* group populations, although five studies to date have revealed some surprising indications of diversification. Moritz's (1987) study demonstrated that populations from Oceania were unisexual (*pelagicus*) and the Pacific Rim populations harbored at least three different bisexual populations, two of which occurred in Papua New Guinea. Subsequently, Donnellan and Moritz's (1995) electrophoretic data identified two major clades in the *pelagicus* group of bisexuals. The clade with the most samples included three lineages: (1) Vanuatu to Madang, (2) Sideia (Milne Bay), and (3) Amelei (New Britain). The second clade also included three lineages, although

each was genetically distinct from the others: (1) Australia (*N. cheverti*), (2) Waro (Southern Highlands), and (3) Utai and Madang (northern PNG coast). These results suggest the possibility of five taxa for Papua New Guinea (Figure 10A). (Note that Donnellan and Moritz did not deposit their specimens in AMS until after publication, so my association of specimens derives from AMS records and the assumption that the specimens that I examined from their localities are the ones used in their study.)

Jackman et al. (2008) provided the first molecular phylogenetic analysis of *Nactus*. This study included only a single sample of a New Guinea *pelagicus* group member and hence offers no information on the relationships among New Guinea populations. Subsequently, this research team (Heinicke et al., 2010) enlarged their sample of New Guinea *Nactus*. Their analysis (Heinicke et al., 2010: fig. 4) revealed two major clades within the bisexual *pelagicus* group. One clade contained all the miniature New Guinea species (*N. acutus*, *N. sphaerodactylodes*, *N. vankampeni*) and populations of the old *pelagicus* taxon that included unisexual and bisexual populations. The unisexual samples were all closely related, although with some minor genetic divergences among the insular populations. The unisexual populations and the bisexual *N. multincarيناتus* were sister taxa and formed one lineage within a clade with another lineage containing the sister pair of *N. cheverti* and *N. galgajuga*. The preceding clade was sister to the Australian *N. eboracensis* and a southern New Guinea population (Gulf of Papua coast). I have not located the two gulf coast specimens, although my sample (#59) derives from the same sample locality.

Subsequently, Zug and Fisher (2012) added additional north coast samples to the Heinicke et al. genetic set. The new samples did not alter the basic clades and added more resolution to the PNG north coast *pelagicus* unisexual-bisexual lineages. This phylogenetic analysis (Figure 10B) revealed (1) a Madang area bisexual population related to *N. multincarيناتus*; (2) a clade of three genetic lineages geographically centered on the Madang area; (3) the genetic distinctiveness of a Morobe Province (Kamiali) population, sister to the preceding unisexual populations, the two Madang bisexual populations, and *N. multincarيناتus*; and (4) a new species (*N. kunan*) of boldly colored *Nactus* that is sister to the Australian *N. cheverti*-*galgajuga* lineage.

The preceding summary of genetic results identifies several aspects about New Guinea *Nactus*: (1) Two distinct clades of *Nactus* occur in New Guinea, a group of miniature species (*vankampeni* group) and a group of moderate- to large-bodied *Nactus*. (2) The latter clade contains two significantly different (genetically) lineages, and each lineage contains both Australian and New Guinea species. (3) The presence of a minimum of four distinct bisexual populations in PNG. (4) The “*pelagicus* complex” as it has been broadly used (as in the title of this monograph) is polyphyletic, and its use should be restricted to unisexual species and their parental species, of which only one (*N. multincarيناتus*) is known. These molecular studies provide

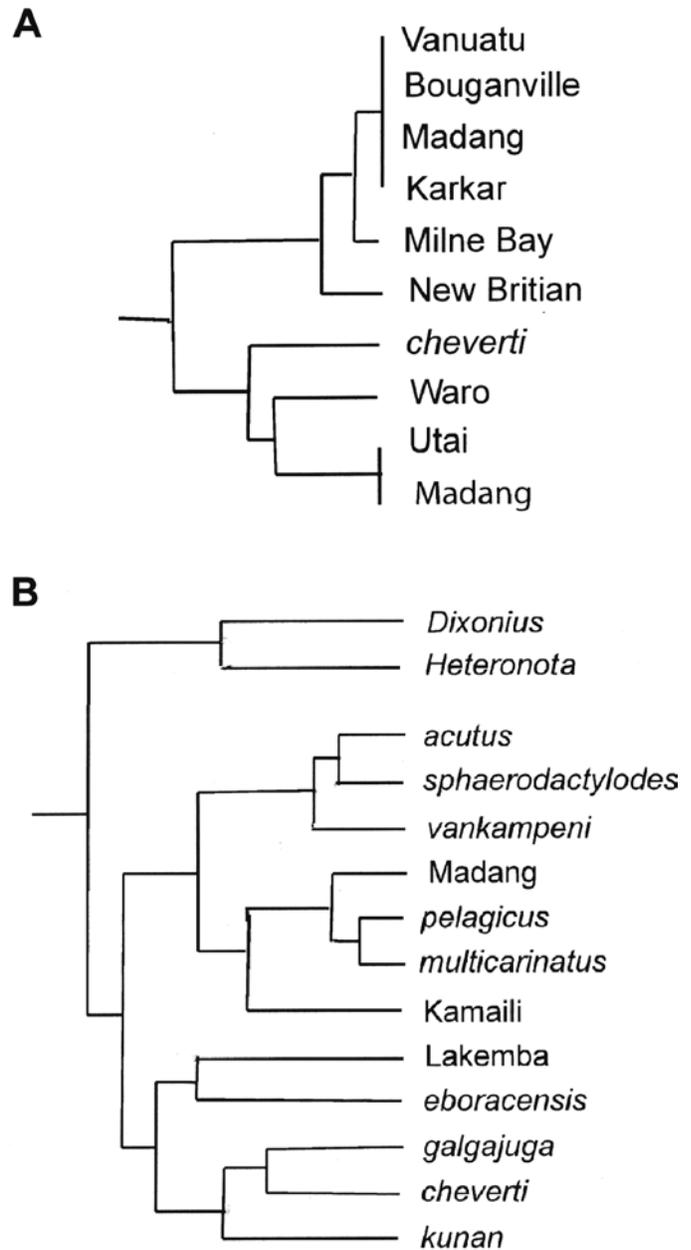


FIGURE 10. Generalized dendrograms of hypothetical genetic relationships among samples of southwest Pacific *Nactus* populations. (A) Summary relationships based on allozymic analysis as proposed by Donnellan and Moritz (1995: fig. 3). (B) Proposed phylogenetic relations based on mtDNA and nuclear DNA sequence data (Zug and Fisher, 2012: figs. 2, 3).

a morphologist with means to identify individuals (vouchers) of the different genetics stocks, thereby potentially assisting in the identification of morphological traits that may differentiate genetic groups.

DISCRIMINATION OF UNISEXUAL AND BISEXUAL POPULATIONS

There are two islands (Manus and Bougainville) within the New Guinea region that harbor unisexual populations of *Nactus* and perhaps a third (Mussau, St. Matthias Islands). Their origins in both time and space are unresolved. Perhaps future genetic studies will answer both questions. For the present, I suggest that both Manus and Bougainville populations are recent introductions and are likely associated with the transport of war materials during World War II because I have found no voucher specimens collected prior to 1940. Both islands sequentially housed both Japanese and Allied troops. The former would seem to be the source for both given that they would have been supplied from ports within Micronesia (e.g., Palau, Chuuk, Guam), which have resident populations of unisexuals, whereas Allied troops derived their supplies largely from Australia or Vanuatu (i.e., Espiritu Santo has only *N. multicarinatus*).

Morphological data suggest an independent origin of both and not a sequential origin from one island to the other. The Manus and Bougainville unisexuals differ but not greatly. Body size ranges and means are equivalent (56.7 vs. 57.0 mm SVL). TrunkL is less in the Manus sample (means of 21.8 vs. 24.5 mm), and this difference is also reflected in the proportion TrunkL/SVL, 38.4% versus 43.0%. Head measurements and proportions are nearly identical in the two populations. For scalation, most traits are equivalent between the two populations, but there are a few differences. Manus unisexuals have larger postmentals (medians of 11.1 vs. 8.2), fewer rows of dorsal tubercles (15.2 vs. 17.4 TubRow), and more forefoot and hindfoot lamellae (19.8 vs. 17.2 and 24.3 vs. 21.3). Interestingly, the Manus unisexual sample has nearly equal numbers of one- and two-spurred (CloacS) individuals, in contrast to the Bougainville unisexuals with only a single spur for all except one individual. The preceding data are also presented in Tables 3 and 4, samples 26 and 33. Some Manus females have precloacal pores; no Bougainville females do.

The samples from these two were collected a decade or more prior to the genetic sampling and so cannot be tested for genetic differences. The variation between these two insular populations, however, hints at different geographic origins and/or localized selection on unisexual populations. Such selection may be widespread and may suggest a greater genetic variation in this widespread parthenogenetic species. Further, this “intraspecific” variation and the broad variation among the New Guinea bisexual samples do not provide a single feature or set of traits that permit the ready differentiation of a female bisexual individual from a unisexual one.

GEOGRAPHIC PATTERNS OF MORPHOLOGICAL VARIATION

Geography of Size and Shape

This section and the following one on scalation are an attempt to recognize and define characters in a regional setting that reflect differentiation of populations. As noted in the

Morphology and Variation section, my samples are variable in size, often small; hence, the latter samples may not reflect accurately the characteristics of those geographic populations.

Adult size (SVL) differentiation exists (Table 3). The Central Province savanna *Nactus* (samples 56, 58) average 43 mm SVL (37–48 mm, $n = 33$). Other samples also have means that do not exceed 48 mm SVL: samples 3, 4, 5, 6, 8, 13, 19, 37, 43, 44, Milne Bay morph C, and 68 (Biak, Yeretuar, Toem, Utai, Sepik-Wagu, Alexishafen, Collingwood, Conflict Group, Wamena, respectively). These samples consist of one, two, or three individuals except for Toem ($n = 6$). Twenty-seven samples have mean SVLs between 49 and 55 mm (samples 1, 2, 7, 9, 10, 11, 12, 14, 15, 20, 21, 23, 24, 40, 41, 42, 43, 47, 48, 49, Milne Bay-B, 52, 55, 64, 66, 67, 68; see Table 3). Combining these populations (samples) with the preceding small-mean SVL ones, the *Nactus* from the north coast of New Guinea from the Vogelkop to the Huon Peninsula and the south coast populations from the Western Province into Papua Indonesia are smaller than the adults from the western third of New Guinea. Large *Nactus* (mean SVL > 60 mm) occur in samples 22 (Madang Province), 27, 28, 31, 32, 33 bisex (preceding [27 through 33] Bismarck Archipelago), 34, 35, 39, 45, 46, 48W, Milne Bay-A, Milne Bay-D, and 51 (latter [34 to 51] from Morobe into Milne Bay Province). Within these samples, a few samples (34, 45, 46, and Milne Bay-A; Kamiali, Misima, Sudest, and Milne Bay A, respectively) have mean SVL > 65 mm to a maximum SVL > 70 mm. These four samples represent two mainland north coast populations and two insular populations of the Milne Bay Province. The largest *Nactus* was a female from Yela (Rossel Island, #48) with 82.1 mm SVL in a sample of adults ranging from 46 to 82 mm SVL. Most of the remaining samples of the western north coast through to the Western Province had average SVLs within the range of 50 to 60 mm and predominantly ≥ 55 mm.

The body and head proportions display a high level of uniformity within and among samples (Tables 3, 4). I observe no evidence of differences between large- and small-bodied samples.

Geography of Scalation

Amid the head scalation, only postmental size (Postm), rows of genial scales between the postmental and infralabials (PmLab), and numbers of supralabial (Suplab) and infralabial (Inflab) scales have a full complement of data for all my samples. I noted earlier that Rösler et al. (2005) suggested several other features of head scalation that may be of diagnostic use. I was able to evaluate only two of the Rösler traits on an intrasample and regional basis. Neither supranasal size and their midline contact nor the number of postnasal scales displayed regional variation, and both displayed broad variation within samples. I conclude from the preceding levels of variation that these two characters are not useful for sample or population differentiation. Similarly, the variation of Suplab and Inflab and my concern with the consistency of my data gathering eliminate them as diagnostic characters.

In contrast, the size of the postmental is geographically variable and of moderate variation within samples. Before examining the New Guinea data (Table 5), it is necessary to examine the variation observed by Eckstut et al. (2013) in Tanna, Vanuatu, populations of bisexual and unisexual *Nactus*. These authors coded their Postm and PmLab characters differently from my coding; however, their coding is easily converted to my coding. They demonstrated that the Tanna bisexual population (*N. multicaarinatus*) always has large postmentals (area ≥ 10) and no PmLab. In contrast, the unisexual population (multiple samples of *N. pelagicus*) has small postmentals (area ≤ 10) and no or one or more rows of genials between the postmentals and supralabials. Their data confirm for Tanna that bisexual and unisexual individuals can be differentiated. This paired characterization holds for most Pacific populations of *N. pelagicus* and Vanuatu populations of *N. pelagicus*. It is less successful for the Manus unisexuals (i.e., 8–18 Postm and 0 PmLab). Bougainville unisexuals have 6–14 Postm and 1–2 PmLab, largely matching the Vanuatu unisexuals.

The St. Mathias–Mussau sample (#27) consists of three adult females, which lack postmentals (Postm = 0). Thus, it seems possible that the Mussau sample represents a unisexual population; however, its small sample size and the continued presence of large areas of native forest on the island argue against assuming that a bisexual *Nactus* “*pelagicus*” population does not exist on Mussau. The Mussau sample (27) was collected prior to World War II, so the argument of an introduction of a unisexual associated with the movement of military supplies is not applicable. A 2014 biodiversity survey of Mussau (Richards and Aplin, 2015) found a few female *Nactus*. These individuals were considered remarkably large (the largest was 65 mm SVL) and led to the suggestion that the Mussau–Emirau *Nactus* may represent a new species. No other distinguishing characteristics were presented. Zug and Moon (1995) reported a maximum SVL of 70.5 mm for Oceania *N. pelagicus* populations.

Elsewhere, the absence of postmentals occurs sporadically and rarely in Papua New Guinea samples until the Fly River area. There most individuals lack postmentals. This uniformity suggests that these samples (64–66) represent a unique population.

The number of longitudinal rows of dorsal tubercles (DorsTub) ranges from 11 to 20 (median values). Large samples ($n = 10$) have median values ≥ 14 . This median value applies also to smaller ($n = 2$ –10) samples. Only the Central Province savanna samples (#56, 58; $n = 36$) has a lower median of 13 (range of 11–14) rows. This latter sample is thus the only sample being a geographic outlier, if only slightly so.

The number of tubercles in a parasagittal row (TubRow) similarly has the Central Province savanna samples (56, 58) with the lowest median, 24, among the 30 samples with 10 or more individuals (Table 5). The range for these larger samples is 24 to 36 (medians), with the median for this group of samples equal to 29.5 TubRow. The lower TubRow counts are scattered throughout PNG; in contrast, the higher counts (medians ≥ 33) occur in western samples (10, 12, 60, 64, 66).

The number of tubercles across the hips (TubHip) averages 8 or 9 rows for most samples. The overall range for all samples is 7–11; however, the low and high counts are rare. There is no evidence of a geographic focus.

The presence of tubercles on the dorsal surface of the hindlimb (TubHindl; Figures 9, 10) and the relative density of the tubercles (TubDens), if present, display a constancy within most samples and variation between localities. The absence of TubHindl occurs in samples from localities 4 through 13, 19mini, 22, 25, 46V, Milne Bay C, 59, and 62 to 69 (Table 6), although not necessarily in all individuals at those localities. Of these samples, 46V and 59 have a few individuals also with tubercles on the crus. Tubercles on both the thigh and crus (TubHindl = 2) is widespread, occurring in samples 1–3, 9, 11, 16–20, 23–24, 26–44, 46U, 47, 48W, 49A, 49B, 51A, 51D, 52, 53, 53D, 54A, 54D, 55, 57, 60, and 61. Of these latter samples, a few contain some individual with no tubercles (samples 9, 10, 19, 60, and 61) or tubercles on only the crus (samples 14, 15, 16, 18, 21, 26, 42, and 56). Only the large Madang coast sample (15) includes one locality, Bogia ($n = 2$), in which all individuals have tubercles above and below the knee.

Where two TubHindl states are present in the same sample, two possible interpretations exist. The first involves the span of time over which data collecting occurred and whether I was consistent in my recognition of the states throughout. The second is the actual presence of individuals with two different traits in a sample and whether this presence represents genetic variation within a single population or denotes two different populations. All three possibilities potentially exist in my samples, with my data collecting spanning more than 20 years. Can I discern which possibility applies to each mixed sample? The answer is yes, correctly, for some but likely not for all. Fortunately, the mixed-state samples are a minority, 16 of 74 samples (23%).

TABLE 6. Distribution of tuberculate and nontuberculate hindlimbs (TubHindl) among the New Guinea *Nactus* samples. States: 0, no tubercles; 1, tubercles only on thigh; 2, tubercles on both thigh and crus; variable, sample contains individuals with states 0 and 2. There are no mixed samples with states 0 and 1 or 1 and 2.

TubHindl state	Localities
0	4, 5, 6, 7, 8, 13, 19, 22, 25, 48C, 49C, 51C, 54C, 62, 63, 64, 65, 66, 67, 68, 69
1	14
2	1, 2, 3, 17, 20, 23, 24, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 43, 44, 45, 46U, 47, 48U, 48W, 49, 49A, 49B, 50, 51A, 51D, 52, 53, 57, 58
Variable	9, 10, 11, 12, 15, 16, 18, 21, 26, 42, 46V, 55, 56, 59, 60, 61

Before offering my interpretation of the geographic distribution of hindlimb tubercle states, I need to comment further on the morphology of the states. I noted earlier in the Scalation section within the Morphology and Variation section that there were more differences in skin texture of hindlimbs than coded by my three-state characterization. The three-state characterization is an oversimplification of texture diversity, although it is adequate to differentiate populations, specifically in the cases where the morphologies (i.e., populations) lack or have tubercles on the hindlimbs or have a few scattered tubercles on the thigh but none on the crus. What the state 2 characterization does not do is account for the variation in the density of tubercles. Figure 8 displays some of this variation (see Figure 8D–F). Within a single locality, the density is uniform; however, a sample comprising multiple localities may have specimens at different localities with different densities. My notes on specimens are inadequate to address these potential differences. Another variable is that in a few localities, the density of tubercles has the tubercles abutting, thereby eliminating the interstices with small granular scales and creating a uniform tuberculate-thigh surface. Presumably, I consistently coded this condition as state 2, but possibly I incorrectly coded it as state 1. If the high density was repeated on the crus, there is a possibility of misinterpretation, and I may have coded the individual as 0 TubHindl. If the tubercles were present and abutting only on the crus, I coded the character state as 3. I draw attention to this variation in hindlimb tuberculation to alert future researchers of *Nactus* to more precisely define the variation in hindlimb tuberculation.

From a geographic perspective, populations containing individuals without tubercles on their hindlimbs (TubHindl = 0) occur continuously from the Vogelkop neck (localities 4, 5) to the Sepik River (12, 13), although not uniformly so. That is, The Aitape sample (9) has one specimen with hindlimb tubercles. One Nuku (10) individual also has hindlimb tubercles; all Kumnatei (also 10) individuals have a unique tuberculate crus morphology. The Wewak sample (11) is evenly divided between the tuberculate and nontuberculate conditions. One individual (Kubka) of sample 12 has tubercles, and the single Wagu specimen (13) lacks tubercles. Samples 14 and 15 have individuals with tubercles only on the crus, and this condition is shared with about half of the Manam Island sample (16). The without-tubercle condition largely disappears from the north coast, with the exception of two small, but adult, individuals in a Madang area sample (19) and the Lae and lower Markham Valley sample (25). Both of these latter samples possess other traits that differentiate them from the atuberculate individuals to the west, and I consider each a different species. Because of shared similarities in other features (e.g., hindlimb tubercles and the presence or absence of preloocal pores), all atuberculate individuals from the Vogelkop neck (4) to Huon Peninsula likely represent a single species that is syntopic with tuberculate hindlimb individuals from Aitape eastward to the Huon Peninsula (23, 24).

The tuberculate condition is not uniform on the mainland. Three tuberculate morphologies occur. The presence of tubercles

on both the thigh and crus occurs in samples from the north coast (Aitape to Huon Peninsula, i.e., 9, 10, 11, 12, 15, 16, 17, 18, 20, 23, 24). Another tuberculate condition has large tubercles abutting on the thigh and crus; it occurs in the individual from Kumnatei (10) and some individuals from Bom (21). The final tuberculate condition is tubercles only on the crus and occurs in samples from Wewak eastward to Alexishafen and Bom (11, 14, 15, 16, 18). Each of these morphologies likely represents a distinct evolutionary lineage.

The absence of atuberculate specimens reappears in the Hatsfeldthapen sample (15) and subsequently in samples on the way to and including the Siar Plantation (19) in the Madang area and is absent again (21–23, 25–26) until reappearing at Boana (22). The Manus (26) and St. Mathias–Mussau (27) populations are insular ones; the Manus population is definitely unisexual, and the Mussau one is possibly so. I interpret this continuous north coast distribution potentially to represent a single species that is sympatric in some areas with tuberculate populations (i.e., 9–11, 16–18, 20–24). The thigh-crus tuberculate (TubHindl = 2) populations are discontinuous, occurring in Morotai (1) and the Schouten Islands (2, 3) and reappearing in the Aitape area (9, 11), but thereafter, tuberculate and nontuberculate populations both occur from Aitape to Lae (25). A single area (14) in northwestern Madang Province has individuals with tubercles only on the thigh. The immediate question is, Did I miscode the tuberculate condition? Possibly; however, data collection for these IRSNB (Mys) specimens was done during a weeklong visit that included examination of other specimens from that area (e.g., 10, 15–18). Even if miscoded, my data indicate that locality 14 has a different tuberculate condition from other populations to the west and east of it. Both of Madang's offshore localities (Manam, 16, and Karkar, 17) have individuals predominantly with thigh and crus tuberculation, Karkar exclusively so and Manam mixed with states 1 and 2. The latter observation is an argument for miscoding, possibly because of a continual cover of tubercles on the thigh.

All Bismarck Archipelago individuals (samples 28–32) have tubercles on the thigh and crus (state 2). That morphology also occurs in the unisexual and bisexual individuals in Bougainville (#33). On mainland New Guinea, state 2 is solely present in all populations from the Northern Province (#34) to Milne Bay (#49), including the populations on the Trobriand and D'Entrecasteaux Islands, as well as in the Louisiade Archipelago. Only one subset of individuals (#49C) have "naked" hindlimbs (without tubercles; state 0). State 2 also occurs broadly from Milne Bay through the National Capital Province (#54–57), although a few savannah Central Province individuals (#55, 56) have tubercles only on the crus (state 1). The central gulf drainage populations (#59–61) are mixed (states 0 and 2), suggesting the possibility of two genetic entities from Bereina to Kikori. The Western Province and highlands populations are uniform and lack tubercles. The naked hindlimb state also occurs throughout southern Papua Indonesia (#62–67).

Cloacal spurs (CloacS) are present in most specimens, although they are absent in a mature female from Alexishafen

(#18), a mature male from Fergusson Island (#39), and an immature male from Sudest (#46). This rarity suggests abnormal development. Most larger samples have a mix of individuals with one and two spurs. Similarly, there is a mix of individuals with acute and rounded spurs (CSTip). I observed no geographic pattern within spur morphology. An interesting aside is the nearly equal numbers of one- and two-spurred individuals within the Manus unisexual sample (#26).

Femoral pores are a rarity in New Guinea *Nactus*. Although preloacal pores are typical of adult males, a few samples (Tables 2, 5) have adult females with preloacal pores, and these samples occur throughout New Guinea. The presence of pores in females potentially identifies genetically differentiated populations but not necessarily speciation. The exception to that hypothesis may be the following samples: Misima (45), Sudest (46U), Milne Bay mainland (51A), and the Central, Gulf, and Western Provinces (60–62, 66; see Table 2). These samples are small with the exception of #45, 46U, and 60, and they possibly are not reliable indicators of the frequency of occurrence of females with pores within a population. The high frequency in the other population likely reflects genetically unique populations. These seven samples have two geographic foci, Milne Bay and western Papua.

The number of preloacal pores in mature males ranges from 0 to 15 (note that ranges and medians in Table 5 include samples of both adult females and males). Examining male-only samples shows that a few samples from the Madang coast (#16–18, 20, 24) contain males without preloacal pores, and there are three localities (Wewak, 11; Emirau, 28; and Egum Atoll, 42) in which all males lack pores. These three latter samples are small ($n \leq 3$) and hence likely do not represent the actual frequencies in those populations. The five former populations also possess males with pores as well as without pores. The preceding five samples have males with a maximum number of pores ranging to 8 (Karkar Island, #17) and 12 (Alexishafen, #18) pores, although the majority of males have no more than 4 pores. For most populations, the median condition is 5 or more preloacal pores and is more commonly ≥ 8 pores. Geographically, a median of ≥ 7 pores occurs in the northern samples from Morotai (#1) to Maraup (#14); then the north coast samples have a low pore count, before a higher median of 10 pores occurs at Lae (#25) and the median remains high through Normanby (#40). Then, the median is generally low (≤ 6) through the Milne Bay area before increasing to ≥ 7 pores on the south coast (#55–69).

The number of digital lamellae (forefoot, ForefLm; hindfoot, HindfLm) appears to be relatively constant throughout New Guinea (Table 5). The inclusive range for ForefLm is 13–23 lamellae; for HindfLm it is 16–26 lamellae. Within the larger samples ($n \geq 15$), the ranges are typically less broad, usually within 15–21 ForefLm and 19–25 HindfLm, and medians are 16–18 ForefLm and 21–23 HindfLm. The Central Province and National Capital Province savanna sample (#56) is the only sample that lies outside the preceding summary (i.e., median = 13, range = 11–15 for

ForefLm, median = 18, range = 16–20 for HindfLm). The two unisexual samples lie within the typical range but differ from one another: Manus (#25) has median = 20, range = 18–22 for ForefLm and median = 25, range = 21–26 for HindfLm; Bougainville (#36) has median = 17, range = 15–20 for ForefLm and median = 21, range = 20–23 for HindfLm.

The Palm character shows limited variation among the samples, with a total range of 3–7 and most individuals having 5–6. There is no apparent regional differentiation.

The two types of subcaudal scales, smooth versus keeled, are almost always uniform within a sample, and predominantly, subcaudal scales are keeled in each of the New Guinea samples. Smooth subcaudals are a characteristic of Australian *Nactus* (Zug, 1998), and their lower frequency of occurrence in New Guinea samples is summarized here. Sample 15 (Madang coast, $n = 22$) has a single individual with smooth subcaudals, an adult male from Bogia; an adult female collected at the same time has keeled subcaudals. Similarly, the large Alexishafen area sample (#18, $n = 46$) has a single smooth-subcaudal female (BPBM 31467) from Baileta; she also differs from other sample members in two other characters. One male (MCZ R98759) from the Finisterre Range (#22) has smooth subcaudals, and the Lae sample (#25) is predominantly smooth (i.e., six of seven individuals). The Mussau sample (#27) has two of three individuals with smooth subcaudals, in contrast to all keel-tailed individuals from Emirau (#28, $n = 6$) and New Ireland (#30, $n = 24$). Three individuals from New Britain (#31, 32, $n = 48$) have smooth subcaudals. The Kamiali sample (#34, $n = 11$) has two smooth-tailed individuals, and Goodenough (#38, $n = 7$) has a smooth-tailed individual. The westernmost sample, Sudest (#46), contains a midsize species ($n = 15$) with keeled subcaudals and a large species ($n = 2$) with smooth subcaudals. The Rossel-Yela sample (#48, $n = 15$) has five smooth-tailed individuals, which likely represent a large-bodied species, and 10 keel-tailed individuals, which likely represent a midsize species. Within the Milne Bay samples, there are three subcaudal states: all subcaudals are keeled, all are smooth, and subcaudals are smooth at the base of the tail but keeled in the posterior two-thirds. These three traits generally also match different sets of other scalation features and body size. All samples to the west of Milne Bay (i.e., 55–69) have keeled subcaudals.

Do one or two individuals with smooth subcaudals within an otherwise keel-tailed sample indicate a genetically mixed sample? In some instances, I believe that is the situation, especially when there are one or more other traits varying in a concordant fashion. The latter is my interpretation for several of the Milne Bay samples. In other samples, particularly among the north coast samples (1–43), one or two smooth-tailed individuals represent either developmental variation or my miscoding during data capture. The latter is not presently resolvable because the specimens are not at hand. The exception to this interpretation is the Lae sample (25) with smooth subcaudals; these individuals suggest a different genetic population.

TAXONOMIC DECISIONS

Only three names are available for New Guinea members of the *Nactus pelagicus* group: *Gymnodactylus (Heteronota) arfakianus* Meyer, 1874 from Yapen Island; *Gymnodactylus heteronota* Boulenger, 1885, a replacement name for *Heteronota fasciata* Macleay, 1878 from Hall Sound, Papua; and *Gymnodactylus pelagicus undulatus* Kopstein, 1926 from Elat, Pulau Kei-besar. The preceding morphological analysis identified characters that show these three names represent unique populations of *Nactus*. That uniqueness is demonstrated subsequently in this section. First, I must note that my conclusions differ strikingly from Rösler et al. (2005). A major difference is that my data support numerous loci of regional differentiation. I will not contrast my interpretations of differentiation and speciation with those of Rösler and colleagues other than they recognized four potential mainland species, two with north and south coast representatives. My data indicate greater regional differentiation and no bicoastal species.

Before proceeding with a geographically clockwise examination of differentiation among bisexual populations, I emphasize that I have not discovered a single character or a set of characters to segregate New Guinea unisexual and bisexual populations from one another. The two unisexual populations (Manus, 26, and Bougainville, 33) differ from one another, although not greatly, and our earlier suggestion (Zug and Fisher, 2012) that the Manus population is an outlier of the Oceania *N. pelagicus* population is likely incorrect. An earlier proposal (Zug and Moon, 1995) for the segregation of unisexual Oceania *N. pelagicus* and bisexual Vanuatu *N. multicarinatus* was that the former had small to moderate postmentals (Postm < 12) and postmentals usually not in contact with infralabials (PmLab = 0), usually a single cloacal spur on each side, and a higher number of hind-foot lamellae (HindfLm 21–25). The Manus Island unisexuals have moderate to large postmentals (8–18) that always contact the infralabials, mostly two cloacal spurs, and mostly individuals with 24–26 toe lamellae. These states contrast sharply with those of the Bougainville unisexual sample that are more similar to Oceania *pelagicus*, having modest-sized postmentals (most with ≤ 8 Postm) usually separated from infralabials (1–2 PmLab) and fewer toe lamellae (21–23 HindfLm). The Bougainville unisexuals thus match the Oceania ones and may represent an introduced population. I can only call attention to this quirky situation and suggest some possibilities: (1) Our Manus Island sample of *pelagicus* is actually from a bisexual population from which only females were vouchered, (2) it is a unisexual population that arose from a different hybridization event than that creating Oceania unisexual *N. pelagicus*, or (3) the differences result from a founder effect with each lineage's subsequent adaptation to local conditions. I also call attention to the presence of three genetic signatures among the unisexual samples of *Nactus* (Zug and Fisher, 2012). A side issue is the origin of the type of *N. arnouxii*. Kluge (1983) suggested the likelihood of

New Caledonia being the actual origin of the holotype, not New Zealand. Kluge also mentioned that the holotype (MNHN 5210) possessed large postmentals, which suggests that this specimen may actually be a female of a bisexual population and hence unlikely to be from New Caledonia.

Returning to the examination of bisexual populations, the two individuals from Morotai (locality 1) share a moderate adult body size (50 mm SVL) and keeled subcaudals with other north coast Papua Indonesia populations; however, they differ from north coast populations by smaller postmentals, fewer rows of dorsal tubercles, and fewer precloacal pores.

The first New Guinea population of *Nactus* to be recognized was the Yapen Island population, *Gymnodactylus arfakianus* Meyer, 1874. The holotype of this species was destroyed in the Allies' bombing of Dresden during World War II. No additional specimens of Yapen *Nactus* have been deposited in museum collections, so I am unable to characterize this population with certainty. Because Yapen likely was connected to Biak and Numfoor during the recent lowering of sea level, I assume that these islands share the same *Nactus* species and assign the name *G. arfakianus* to the Schouten Islands' populations. For the present, I characterize this taxon on the basis of two adult females, one each from Numfoor and Biak. I note the similarity of *N. arfakianus* to the distant and isolated Morotai population, but I am allowing geography to bias my decision to recognize two species. Although similar to the mainland samples (4–8) of the northern coast, *Nactus arfakianus* differs from those populations in the number of precloacal pores and the presence of tubercles on the thigh and crus, which they lack.

The mainland samples include two samples (4, 5) from the area south of Cenderawasih Bay. These localities lie on either side of the isthmus (or neck) of the Vogelkop Peninsula. Although they are similar in body size and most scalation features, I tentatively consider each to represent a different taxon owing to the absence of a postmental and fewer dorsal tubercles in the Yeretuar individual (#4) in contrast to the Nabire (#5) to Toem (#6) specimens. The populations (samples) from Nabire to the Huon Peninsula (#24) represent multiple species. Most samples are homogeneous, containing individuals of the same species, although some are mixed, which likely signals sympatric species or ones occurring in close geographic proximity (possibly parapatrically).

A combination of characters suggests that samples 5 through 13 include mostly individuals that represent a single species ("*septentrionalis*"). These individuals share hindlimbs without tubercles (TubHindl = 0), keeled subcaudals, males having ≥ 8 precloacal pores, and modest body size (SVL range of 42–58 mm). Some samples are not homogeneous. The Torricelli Mountains sample (10) includes a second group of individuals sharing a unique morphology and differing from the *septentrionalis* morphology. Sample 10 combines six localities along the mountain range and adjacent lowland. The individuals from Kumnatei (IRSNB 15802A-S) have a TubHindl morphology of

largely closely packed large tuberculate scales without small interspersed granular scales. These specimens are presently unavailable to me, so I cannot confirm their uniqueness relative to other specimens from sample 10, so I am relying on my decades-old notes; nevertheless, their hindlimb scalation argues for their uniqueness. I recognized these leg-armored *Nactus* from locality 10 and five individuals (IRSNB 15871.137–138) from Bom in sample 21 as a distinct species (“*grevifer*”). Similarly, a specimen (FMNH 14030) from Kubka in the Ambunti sample (12) differs by possessing full tuberculate hindlimbs (TubHindl = 2) and is considered a member of a separate species detailed below. The admixture in this group of samples (11–18) and subsequent groups attests to the sympatry or parapatry of two or more species along the north coast of Papua New Guinea.

I wish to reiterate some observations from pre-DNA molecular data. These data (Figure 10A) similarly suggest two or more species at the same locality or adjacent ones that are not discriminated by the locality data on the museum specimens. Donnellan and Moritz (1995: table 1) recognized three groups of *Nactus* in PNG on the basis of allozymatic data. The Waro population, a Southern Highlands Province locality from the south coast drainage, was unique among their samples. Utai and one Madang specimen represented a second population. Most of their Madang sample represented a third *Nactus* that was linked with an assortment of other north coast populations, for example, Bismarck, Milne Bay, and Vanuatu. They also identified a hybrid individual. Their figure 3, displaying percentages of fixed differences, showed a similar linkage of localities and specimens: Utai and Madang specimens were identical, and most Madang specimens were the same as other north coast populations (Karkar Island, all Bismarck ones, and Vanuatu).

A more recent molecular data set (mtDNA and nuclear DNA sequences; Zug and Fisher, 2012: fig. 2; also see Figure 10B) demonstrated a similar absence of homogeneity among PNG north coast localities, including adjacent ones. Tekadu (a Morobe Province locality in the Lakemba River basin, a south coast drainage system) is distantly related to north coast samples and has modestly close relationships to Australian *N. eboracensis*. On the north coast, the unique Manus Island *N. kuman* is related to the Australian *N. cheverti* and *N. galgajuga*. The north coast samples showed three lineages: (1) a bisexual one with Madang lizards related to Vanuatu *N. multicarinatus*; (2) a bisexual branch with two distinct Madang populations, one with affinities to Samoan *N. pelagicus* and another distinct Madang population; and (3) a more distantly related bisexual population from Kamiali. Both molecular data sets confirm the presence of multiple unique populations of *Nactus* on the north coast, although rarely can I firmly link morphological differentiation with the molecular patterns.

The presence of multiple genetic lineages supports my interpretation of multiple unique populations as revealed by the morphological data, although the morphological data do not reveal relationships among and between morphotypes. The north coast from the mouth of the Sepik to and including the Huon

Peninsula appears to contain four bisexual species of *Nactus*. Further, as noted above, some localities have two or three species co-occurring.

The first of these northern PNG coast morphotypes consists of individuals sharing tuberculate hindlimbs, occurring in the samples from Aitape, Torricelli Mountains, Wewak, Sepik-Ambunti, Madang, Manam, Karkar, Alexishafen, Madang, Guisko, and Finschhafen (samples 9, 10–12, 15–18, 20, 23, 24). This set of individuals (“*allenallisoni*”) also possesses keeled subcaudals, adult males with few (≤ 2) or no preloocal pores, modest numbers of dorsal tubercle rows at the midbody (≤ 13 DorsTub), and moderate body size (49–62 mm SVL). The hybrid individual (AMS 124028; Donnellan and Moritz, 1995) occurs within this set of individuals and share the *allenallisoni* morphotype. These 11 samples are predominantly coastal plains and adjacent insular ones. They span a distance of more than 700 km and overlap or are adjacent to populations of several other species, for example, co-occurring with *septentrionalis* at localities 9, 10, 11, and 12 (Aitape, Torricelli, Wewak, and Ambunti).

Another group of individuals (Wewak, 14–16; NW Madang mountains and coast, 18; Manam, 21) also occupy north central coastal Papua New Guinea. These individuals (“*aktites*”) possess keeled subcaudals, adult males with a modest number (2–7) of preloocal pores, tubercles only on the crus, and moderate body size (44–61 mm SVL).

One of the north coast sample localities (#18) contains a major mixture of species. This sample consists of individuals from Alexishafen and Siar Plantation (north of Madang). The majority of the individuals are either *allenallisoni* or *aktites*. Three individuals, however, represent neither of these two species. One of them (AMS R124028) was identified by Donnellan and Moritz (1995) as a hybrid, although a hybrid of what species was not clear because they did not recognize more than a single genetic population (no. 5 in their table 1) in this area. One of the parental species is *allenallisoni* based on the hybrid’s morphology, and presumably, an *aktites* was the other parent. In their voucher collection, they did not analyze AMS R124051 and R124053 (identifying one or both as *N. vankampeni* or juveniles). These two individuals are a mature female and male (36.6 and 44.8 mm SVL, respectively) and represent a distinct miniature species (“*nanus*”).

The *allenallisoni* morphotype reaches the tip of the Huon Peninsula but seemingly does not cross the mountain range into the Markham Valley, as individuals from Boana (#22) and Lae (#25) are morphologically distinct from *allenallisoni* and other north coast species. These Markham Valley individuals lack tubercles on the thigh and crus and possess smooth subcaudals, in contrast to the other nearby north coast species and populations occurring both east and west of them. They also appear to average larger than the Huon *allenallisoni* population; however, they are not as large as the nearby Kamiali population (#34). I recognize them (#22, 25) as unique (“*intrudusus*”) among the other mainland species.

In the sea to the north, Manus Island (Admiralty Group) has two *Nactus* (Zug and Fisher, 2012), the boldly colored *N. kunan*, whose closest relative is *N. galgajuga* of the Cape York Peninsula, Australia, and *N. pelagicus*, a unisexual population. The outlier islands (St. Matthias Group) of the Bismarck Archipelago, Mussau (#27) and Emirau (#28) are about 25 km apart; the latter is represented in my sample by only two adults; the former is represented by six adults. There appears to be no morphological difference between these two populations or between them and the closest other Bismarck population (30, New Ireland). No specimens were available from New Hanover (29).

The two New Britain samples (31, 32) are identical to one another as well as to the New Ireland and bisexual Bougainville samples. I interpret this similarity as representing a single species (“*robertfisheri*”) for the Bismarck Archipelago and Bougainville. These populations (i.e., *robertfisheri*) share keeled subcaudals, usually a moderately large postmental (Postm \geq 10), and tuberculate thigh and crus. Most males have a moderate number of precloacal pores (usually \leq 7). There are, however, a few adult males (AMNH 104966, MVZ 40779, MVZ 40781, and USNM 120881 from Emirau and BPBM 22024 and BPBM 22029 from New Britain) lacking pores and five New Britain adult males (BPBM 22013–014, 22017, 22024–025) with only 1 to 5 pores. Do these individuals represent a different genetic entity, or am I placing an overly segregating emphasis on this difference in pore number? I cannot answer this question with my other morphological characters, so I wish only to call attention to the possible occurrence of a different species among the more abundant *robertfisheri* individuals.

Before returning to the mainland, I need to examine the question of whether the Bismarck populations (i.e., *robertfisheri*) are different from or the same as the Vanuatu *N. multicaarinatus* populations. Once *N. multicaarinatus* was resurrected for South Pacific bisexual populations, its name became the identifier for the New Guinea bisexual population (e.g., Heinicke et al., 2010). Even earlier (Donnellan and Moritz, 1995), Bismarck and north coast populations were considered conspecific with Solomon-Vanuatu populations. My preceding demonstration of morphological differentiation among many north coast Papua New Guinea populations argues that *N. multicaarinatus* is not a resident of the north coast; however, this conclusion is not applicable to Bismarck bisexual populations, which differ from the preceding populations (species) but morphologically match our (Zug and Moon, 1995:88) characterization of *N. multicaarinatus* based on Vanuatu populations. Among my meristic characters, these two sets of populations differ only in the slightly higher number of finger and toe lamellae. Bismarck populations commonly possess more. Are these two traits sufficient evidence for recognition of specific differentiation? For me, yes! Specific recognition is always a hypothesis, and in this instance, it will require testing with molecular data.

On mainland New Guinea, the Kamiali (34) population possesses a number of similarities to the Bismarck populations (27–33) and the *allenallisoni* populations (9, 11–12, 14–18, 20,

23, 24), although differing from them by a modal larger body size (62–73 mm SVL versus 48–71 mm SVL for *robertfisheri* and 48–64 mm SVL for *allenallisoni*), and males always possess precloacal pores and more than 8 pores. The populations east of Kamiali (Mount Lamington, 35, and Popondetta, 36) are represented by three individuals and, despite being smaller, are within the size of range of Kamiali individuals and match them in other features of scalation. I suggest that these populations (34–36) represent a unique genetic entity (“*kamiali*”).

Nearing the Milne Bay area and adjacent island groups, adult body size (45–53 mm SVL) drops in the Collingwood Bay samples (37); otherwise, their morphology generally matches the *kamiali* populations. The significantly smaller average SVL argues against their inclusion in a strict *kamiali* paradigm. They also average smaller than the insular populations of Goodenough Island (38) and Fergusson Island (39); although a few adult females of the latter two samples are within their size range, no adult males are. The closest mainland samples (49–53) at the eastern tip of mainland New Guinea also are generally larger except for a single population (“C,” a unique morphotype in samples 49, 50, 51; see Table 3) that is distinctly smaller. These differences from adjacent and more distant populations are insufficient to suggest differentiation from adjacent populations. I tentatively attribute the smaller size to the vagaries of sampling, yet I hesitate to identify them as members of *kamiali*.

The Milne Bay area samples (38 to 54) contain populations with multiple levels of morphological differentiation and, in several samples, two or three morphotypes. The first insular Milne Bay samples (Goodenough Island, 38, and Fergusson Island, 39) share characteristics with one another and, aside from a smaller average size and fewer rows of dorsal tubercles (DorsTub = 13–18 vs. 17–20), with the *kamiali* samples (34–36). These insular populations also usually share larger postmental scales and more variable precloacal pore numbers than *kamiali*. Although the differences are less than those observed in other north coast populations, I still considered them distinct from the *kamiali* populations. As I broaden my review of character variation in the Milne Bay samples, I began to view *kamiali* as geographically widespread on the northwestern coast of the mainland at least as far west as the Collingwood Bay area, thus occupying much of Morobe and Oro Provinces. Perhaps, the large body size of the individuals from the vicinity of Kamiali results from either the field sampling in the Kamiali area or the diet of individuals from a less disturbed rainforest area.

Moving farther west, there are no samples from the north coast of Milne Bay Province, although there are numerous ones from the islands. My interpretation of differentiation within the north insular populations of Milne Bay (38–43, Goodenough to Woodlark) has varied from differentiation from *kamiali* to similar except for size. This size difference has led me to view them as different genetic entities from *kamiali*. These insular populations also share similarities to the most common Milne lowland *Nactus* (comprising most of the individuals in samples 49–55). Owing to my uncertainty of their affinities to either *kamiali* or

the lowland Milne Bay population, I refrain from assigning a specific name to these populations.

Contrasting the Goodenough (38) and Ferguson (39) populations with the Normanby one (40) on the same submarine bank (i.e., D'Entrecasteaux Archipelago), the Normanby *Nactus* has a smaller median body size (53 mm, range = 45–64 mm SVL vs. 60 and 66 mm, respectively) and smaller postmental scales (Postm = 2–18, all but two have ≤ 12), suggesting differentiation. Proceeding farther offshore, the Trobriand sample (41) is not greatly different from the D'Entrecasteaux populations, differing only in a lower number of preloacal pores (1–9; all but one has 5 or fewer pores); however, the average and range of SVL are lower, and additionally, the sample is sexually dimorphic (i.e., males are smaller than females). The samples from Yanaba (42) and Woodlark (43) match the morphology of the Trobriand individuals. More distantly on the Trobriand bank of atolls and islets, the samples from Panaeati (44) and Misima (45) differ from one another. Panaeati *Nactus* are considerably smaller (44–50 mm SVL) than those of Misima (52–77 mm SVL); also, the latter possesses fewer rows of dorsal tubercles and more preloacal pores. Even though the size ranges of the two populations nearly overlap, most (84%) of the Misima sample have a SVL greater than 63 mm. The Misima sample also possesses fewer preloacal pores (2–7 vs. 7–8) than the Panaeati sample. I recognize each insular population as a distinct species (“*panaeati*” and “*fredkrausi*”).

The outermost islands (samples 46, Sudest; 47, Nimowa; 48, Rossel) and their samples offer a challenge for the interpretation of differentiation within and among these three islands. My first segregation of populations derives from the presence of individuals with smooth versus keeled subcaudals. The latter is the typical condition for most New Guinea populations of *Nactus* (Table 7). The former is characteristic of Australian *Nactus*, although the trait also occurs in New Guinea in the Markham Valley *intrudusus* and in two populations on mainland Milne Bay. The smooth state occurs at low density (12%) in Sudest, slightly higher frequency (28%) in Rossel, and not at all in Nimowa. At the localities with smooth-subcaudal individuals, those individuals are the largest adults in all the samples, 76–78 mm SVL at Sudest and 67–82 mm at Rossel, in contrast to 48–65 and 46–60 mm, respectively, for the keeled-subcaudal specimens. Do these island pairs represent two or four species? Because the islands are each located on separate submarine volcanic peaks and separated by wide and deep marine channels, geographic isolation suggests four species; however, the interisland small and large pairs each possess a unity of characteristics. Because of the shared characteristic within each of these pairs, I propose two species, a moderate-sized species and a large species, “*modicus*” and “*amplus*,” respectively.

The pattern of character differentiation on mainland Milne Bay (samples 49–54) is no less complex than in the islands. I recognize three distinct morphotypes: totally keeled subcaudals, keeled subcaudals at the base of the tail but smooth thereafter,

and totally smooth subcaudals. The smooth-subcaudal individuals also differ from the others by a smaller adult body size (31–45 mm SVL). These small individuals (“*chrisaustini*”) were present at three sample localities (Alotau-lowlands, 49; Owen Stanley, 51; Fife Bay, 53), which may result from geographic coding but likely depicts a broader occurrence along the southern edge of the Pini Range. This small species is sympatric with a larger species that has a similar distribution (51, 53), but it appears to be more abundant, that is, has a larger sample ($n = 22$ vs. $n = 8$ for *chrisaustini*). This larger morphotype also occurs at more sites within the two sample localities, suggesting a distribution from Sideia to Fife Bay, apparently occupying the forest of the southern lobe or peninsula of Milne Bay. It (“*notios*”) possesses subcaudals that are keeled basally and then smooth on the posterior two-thirds of the tail. It is moderately large (52–71 mm SVL, not sexually dimorphic), and only males possess preloacal pores. A small ($n = 7$) group of individuals have smooth subcaudals, and both males and females possess well-developed preloacal pores (6–14 pores). They (“*erugatus*”) derive from samples 51, 53, and 54 (Owen Stanley, southern mountains) and are moderately large (59–72 mm SVL). The remaining Milne Bay specimens possess the typical keeled subcaudal morphology (Table 7); specimens derive from all Milne Bay sample localities (49–54), suggesting a predominantly lowland species (“*alotau*”), likely occurring mainly in disturbed forested habitats. I suspect that *alotau* is a composite of two species, although aside from a slight difference in preloacal pore number (4–9 vs. 5–13), I cannot reliably segregate individuals into two groups. The potentially composite *alotau* has an adult size range of 48–66 mm SVL.

The next sample (55, Central Province mountains east) is a composite of several midmontane sites approximately 70–80 km east of the savanna samples (56) of the Central and National Capital Provinces and roughly 50 km east of the nearest Moresby area forest sample (57). Distance from the Milne Bay *alotau* populations would suggest possible differentiation; however, morphologically, these lizards share all the characteristics of the *alotau* population. Further, the forest lizards from lowland and midmontane sites (57) surrounding the Moresby savanna share the *alotau* morphology. The next midmontane sample (59, Tekadu) also matches the *alotau* morphology (molecular analysis has identified this population as being distinct from PNG north coast samples; Heinicke et al., 2010). My interpretation of similarity among these distant populations (Milne Bay to Lakekamu River drainage of the eastern Gulf Province) suggests a single species (*alotau*) of a moderately large forest *Nactus* along the southern front of the Owen Stanley Range.

The Moresby or Central Province savanna *Nactus* is distinctly smaller than the preceding forest species with 40–47 mm SVL for females and 37–47 mm SVL for males. Most individuals display moderate-sized postmentals (≤ 14), few rows of dorsal tubercles (DorsTub = 11–14) and fewer tubercles in the dorsal rows (TubRow = 19–32, majority having ≤ 25), and a variable hindlimb tubercle presence (TubHindl = 1–2, majority with 2);

TABLE 7. Comparison of northeastern coast samples of *Nactus* in which the subcaudal scales are keeled. Values are for all keeled specimens in each sample. The values are ranges. Note that in the first row for each sample locality, the values for the meristic traits are for the entire sample; the SVL of each sample is for adults only. SVL = snout–vent length; Postm = postmental scale size; PmLab = postmental-infralabial contact; DorsTub = rows of dorsal tubercles; TubRow = tubercles in a parasagittal tubercle row; PreclPor = preloacal pores. The meristic trait value for subcaudal scales was zero for every sample.

Sample number, name, and size	Sex	SVL by sex (mm)	Meristic trait values for total sample				
			Postm	PmLab	DorsTub	TubRow	PreclPor
34. Morobe, Kamiali, 12♀+♂	♀♀	62–73	0–18	0–1	17–20	27–33	8–10
	♂♂	68–69					
35. Mount Lamington, 2♀+♂	♀	66	16–19	0–1	18–19	27–30	11
	♂	63					
36. Popondetta	♂	60	18	0	19	31	8
37. Collingwood Bay, 3♀+♂	♀♀	45–53	8–18	0	16–17	25–32	0–10
	♂♂	56					
38. Goodenough Island, 7♀+♂	♀♀	45–62	10–20	0–2	14–17	25–40	13
	♂	64					
39. Fergusson Island, 27♀+♂	♀♀	47–74	6–26	0–1	13–18	26–40	2–12
	♂♂	51–69					
40. Normandy Island, 16♀+♂	♀♀	47–64	2–18	0–1	15–20	24–34	0–8
	♂♂	46–52					
49. Alotau, 19♀+♂	♀♀	49–62	6–20	0–1	13–18	24–34	4–9
	♂♂	43–54					
50. Alotau, East Cape mountains, 13♀+♂	♀♀	59–63	12–16	0–1	16–18	24–30	5–9
	♂♂	59–62					
51. Milne Bay, Owen Stanley Range, 4♂♂	♀♀	61–66	12–18	0–1	16–17	27–30	13
	♂	66					
52. Milne Bay, Sideia, 3♂♂	♀♀	53–59	14–17	0	14–16	24–25	0
	♂	48					
53. Milne Bay, Fife Bay, 5♀+♂	♀♀	57–65	14–20	0	14–20	26–32	12–13
	♂♂	50–58					
54. Milne Bay, southern mountains, 6♀+♂	♀♀	60–66	8–18	0–1	12–17	27–46	9–13
	♂♂	61–66					
55. Central Province, eastern mountains, 13♀+♂	♀♀	53–66	10–22	0–1	13–16	24–31	0–8
	♂♂	49–52					

preloacal pores are absent in females, and males have 3–7 pores and fewer digital lamellae (ForefLm = 11–15, HindfLm = 17–20). The preceding traits also distinguish the savanna population from the surrounding forest species and from the smaller *chrisaustini* of the Milne Bay area. Its uniqueness was recognized by Macleay (1878), and his proposed name was subsequently corrected to *heteronotus* (type locality is Yule Island).

Continuing westward along the Papuan coast, in the Purari River sample (60), most specimens derive from upriver, montane

valley localities. Initial data capture suggested that this population might be an all-female one; subsequently, a few males were discovered (i.e., 6 adult males and 23 adult females). Although unevenly sampled, there is no sexual difference in size (adult SVL = 49–64 mm, most are >55 mm). Other characteristics are as follows: postmental is small to midsize (Postm = 2–18, 76% have 8–12), and TubHindl is either absent (67%) or on crus and thigh (33% of total sample); both males and females have preloacal pores (PreclPor = 0–12 for males, 0–11 for females, and

only three females are without pores). This set of traits differentiates this population from the more easterly *alotau* populations. Individuals from the Aird Hills (61) match the preceding Purari sample, and both are considered representatives of the same genetic population (“*papua*”).

The Torres Strait Islands have a mixture of *N. eboracensis* with smooth subcaudals and a New Guinea *Nactus* with keeled subcaudals (Zug, 1998). Although a TS sample was not a formal part of this study, it can be characterized from data from my 1998 study. The population has nondimorphic adults averaging 48 mm SVL (range = 41–59 mm) and midsize postmentals (median = 14, range = 6–20); all ($n = 14$) but one female lacks preloacal pores, and all ($n = 8$) but one male has pores (6–10). All TS individuals possess tubercles on both the thigh and crus (TubHindl = 2). These features more closely match the *papua* populations to the gulf coast populations rather than the geographically closer “*inundatus*” populations of the Fly delta.

The southern Fly River delta sample (64) and the one west of the Fly delta (66) differ from *papua* and from the two highlands samples (Chimbu, 62; Waro, 63). The Fly *Nactus* are moderate-sized (45–58 mm SVL) lizards and not sexually dimorphic. With only two exceptions in the locality 66 samples, they lack postmental scales; these are the only Papua New Guinea samples with this trait, which appears rarely and usually singly in the other New Guinea samples (see also comments in the Geography of Scalation section). The dorsal tubercle traits and hindlimb lamellae counts match those of *alotau* and *papua*. They differ from those two species by the absence of tubercles on the hindlimbs (TubHindl = 0). Both females and males possess preloacal pores; most females have a third of the number of pores as males. This distribution of characters indicates these two populations represent a unique genetic entity (*inundatus*). Three specimens from this area (MCZ R124313, Lake Murray; AMS R121165, Wipim; MCZ R124299, Boze) differ by the presence of tiny postmentals. Because they match the other *inundatus* specimens in other traits, I assign them to this species.

The two highlands samples derive from two drainage systems: Chimbu (#62, $n = 4$), south coast drainage to Purari River, and Waro (#63, $n = 2$), south coast drainage to Kikori River. This difference in drainages might suggest differences in morphology. Such differences do not exist; the two samples are similar in adult size and all scalation features. Individually, they match the characteristics of the south coast *papua*. For convenience and without certainty, I assign them to this species.

The remaining three samples (67–69) are represented by one specimen each. The Sabang sample (67, ZMA 15379) was examined early in this study, and the state of its postmental was not recorded; otherwise, its traits match *inundatus*. The Wamena individual (#68, BMNH 1978.2180) has a small postmental (Postm = 4), and otherwise, it also matches *inundatus*. Thus, I provisionally assign them to *inundatus*. The single specimen from Greater Kei is a small (37.4 mm SVL) adult male lacking a postmental and possessing a tubercle-free hindlimb, 10 preloacal pores, and a low number of forefoot and hindfoot

lamellae. It is the holotype of *Gymnodactylus pelagicus undulatus* Kopstein and remains the only known *Nactus* specimen from the Kei Islands.

Throughout the preceding discussion of my taxonomic decisions, I have noted my uncertainty about the composition of several of the species that I am recognizing. This overt recognition of uncertainty is not an attempt at face-saving; rather, it is a desire to draw attention to the complexities of the morphological diversity and the co-occurrence of multiple species in some of my samples that represent relatively small geographic loci. Philosophically, I believe that the nomenclatural recognition of a new species is a scientific hypothesis and must be tested by additional data and different techniques.

Finally, although I have used “*Nactus pelagicus* complex” in the title of this publication, I recommend abandoning this concept and label. I recommend labeling cladistics groups. Genetic data (Heinicke et al., 2010; Zug and Fisher, 2012) indicate the existence of four clades: (1) miniature *Nactus* or the *vankampeni* group (*acutus*, *sphaerodactylodes*, *vankampeni*), (2) the *multicarinatus* group (*multicarinatus*, *pelagicus*, which presently encompasses all the known parthenogenetic populations, and likely many New Guinea species with keeled subcaudal scales), (3) the *eboracensis* group (*eboracensis*), and (4) the *cheverti* group (*cheverti*, *galgajuga*, *kunan*). These groups are tentatively characterized by (1) the range of adult SVL, (2) relative postmental size, (3) surface morphology of subcaudal scales, and (4) dorsal trunk tubercle rows.

Molecular phylogenetic studies have sampled only a fraction of the New Guinea populations and have not included the Mascarene *Nactus*, which also have not been included in this study. The preceding four groups may correctly represent the major cladistics branches, although I suspect they do not include the two newly discovered miniature species herein (one in the Madang area and the other in Milne Bay area, both sympatric with larger-bodied *Nactus*). Nonetheless, for the present, the *pelagicus* group paradigm should be abandoned, and we should adopt a cladistic group labeling.

I offer the following characterization of the four groups, recognizing that only the *vankampeni* group is uniquely distinguished. (1) In the *vankampeni* group, average adult SVL ≤ 36 mm, with the maximum rarely exceeding 42 mm; postmental scales are absent, with the area occupied by small genial scales; subcaudal scales are enlarged, smooth, or keeled; there are no rows of dorsal trunk tubercles; members are *acutus*, *sphaerodactylodes*, and *vankampeni*. (2) In the *multicarinatus* group, adult SVL range = 42–64 mm, usually >48 mm; postmental is small to moderate; subcaudal scales are slightly enlarged and keeled; there are moderate to numerous rows of dorsal trunk tubercles, usually 24–36; members are *multicarinatus*, *pelagicus*, and likely most north coast *Nactus* species. (3) In the *eboracensis* group, adult SVL range = 38–57 mm, usually >48 mm; postmental is small to moderate; subcaudal scales are slightly enlarged and smooth or keeled; there are numerous rows of dorsal trunk tubercles, usually <38 ; members are *eboracensis* and Milne Bay

and south coast populations. (4) In the *cheverti* group, adult SVL range = 38–57 mm; postmental is small to large; subcaudal scales are slightly enlarged and smooth; there are numerous rows of dorsal trunk tubercles, usually >40; members are *cheverti*, *galgajuga*, and *kunan*.

SPECIES ACCOUNTS – NEW GUINEA REGION

The species accounts are arranged by geographic occurrence in a clockwise fashion, beginning with the outlying population on Morotai (island) north of Halmahera and then moving to New Guinea proper at the north Vogelkop coast (Sausapor) and ending with the Kei Islands in the Arafura Sea. Geocoordinates in the type description are given in brackets when the coordinates were not included in the original museum catalog entry. For descriptive purposes, for the mean size in all *Nactus* species accounts, small is ≤ 40 mm SVL, moderate is 42–56 mm SVL, and large is ≥ 58 mm SVL.

Nactus arceo, new species Morotai Slender-toed Gecko

HOLOTYPE. BYU 7540, adult male, Morotai [2.3218° 128.4572°], collected on 4 November 1944 by Ernest Reimschuessel (Figure 11).

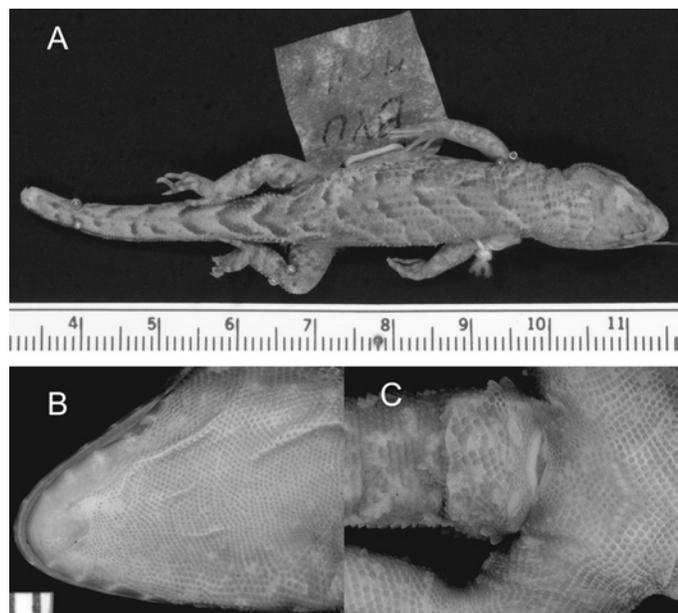


FIGURE 11. Holotype of *Nactus arceo* (BYU 7540). (A) Dorsal view of entire body, (B) ventral view of head (scale is 1 mm), and (C) ventral view of pelvis and thigh. (Photographs by J. Poindexter, USNM.)

PARATYPES. BYU 7331, unsexed juvenile, Morotai [2.3218° 128.4572°], collected on 4 November 1944 by Ernest Reimschuessel.

DEFINITION. A bisexual taxon of geckos (Gekkoinae) of moderate adults (~50 mm SVL) with keeled subcaudals, small postmental scales (6–12), no postmental-infralabial (PmLab) contact, moderate number of dorsal tubercle rows (18–19), and low number of tubercles (25–27) in parasagittal row (TubRow), tubercles on dorsal surface of thigh and crus, and modest number of preloacal pores (9). A diagnostic summary is given in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 50.5 mm SVL, ~36 mm tail length (broken and half regenerated), 20.5 mm TrunkL, 19.3 mm SnForel, 13.8 mm HeadL, 8.8 mm HeadW, 6.4 mm HeadH, 3.6 mm EyeD, 4.4 mm NarEye, 2.2 mm SnW. Body proportions: 41% TrunkL/SVL, 38% SnForel/SVL, 27% HeadL/SVL, 17% HeadW/SVL, 64% HeadW/HeadL, 6% EyeD/SVL, 22% EyeD/HeadL, 30% NarEye/HeadL, 26% Interorb/HeadL, 16% SnW/HeadL.

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal trapezoidal rostral scale with a slight middorsal notch, cleft on midline of middorsal third and distinctly depressed on its mid-posterior half; 3 large supralabials (left and right, Suplab) and 3 infralabials (left and right, Inflab) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 2 moderate size granular loreal scales, dorsalmost one largest. Supranasals moderate size separated on midline by 1 granular scale contacting rostral. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large trapezoidal mental and small elliptical postmentals (Postm = 6). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape to tail; on trunk rows reach ventrolaterally to edge of venter, 18 entire rows (DorsTub), and only to mid-laterally on neck; tubercles in each row usually separated by single granular scale yielding 27 tubercles per row (TubRow); 8 rows transversely between hindlimbs (TubHip). Uniform covering of moderate-sized tubercles on dorsal half of forelimb; hindlimb with numerous tubercles (TubHindl = 2), and tubercles abundant fore and aft (TubDens = 1). Tail with tubercle rows dorsally and laterally. Tubercles uniform and moderated sized. Tail half regenerated, and regenerated portion with uniform, moderate-sized keeled scales (Subcaud = 0). Pair of cloacal spurs (CloacS) on each side, distal edge truncate (CSTip = 0). Ventral scales from chin to vent small, uncarinate, granular and somewhat larger on chest and abdomen. Preloacal pores 9. Forefoot with narrow digits, their lengths $3 \approx 4 > 2 > 5 > 1$ (the notation “ $3 \approx 4 > 2 > 5 > 1$ ” indicates the third digit is approximately equal in length to the fourth digit, which is longer than the second digit, which is longer than the fifth digit, which is longer than the first digit); 15 lamellae beneath fourth digit (4FingLm), 4 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their

TABLE 8. Summary of character states for differentiation of New Guinea bisexual species of medium to large *Nactus*. Range and mean are given for adult SVL, and median and integer range are given for meristic characters of the entire sample. Characters and their abbreviation are identified in Appendix Table A1. Taxa are arranged clockwise from Morotai around New Guinea. A dash (—) indicates either no specimens or no measurement possible. DorsTub = rows of dorsal tubercles; SVL = snout–vent length.

Species (<i>n</i>)	SVL (mm)		Subcaudals	Tubercles			DorsTub rows	Preloacal pores	
	♀♀	♂♂		Thigh	Crus	Postmental		♀♀	♂♂
<i>arceo</i> (2)	—	50.5	Keeled	Yes	Yes	9	18.5	0	9
	—	—	—	—	—	6–12	18–19	—	—
<i>arfakianus</i> (2)	49.6	—	Keeled	Yes	Yes	17	16.5	15	—
	47–52	—	—	—	—	12–21	15–18	—	—
<i>rainerguentheri</i> (1)	47.3	—	Keeled	No	No	0	10	0	—
<i>septentrionalis</i> (42)	49.1	48.7	Keeled	No	No	12	14	0	9
	42–54	42–57	—	—	—	2–18	12–17	0–2	8–12
<i>allenallisoni</i> (116)	56.6	53.2	Keeled	Yes	Yes	14	17	0	2
	47–64	46–63	—	—	—	0–22	12–22	0–3	0–9
<i>grevifer</i> (24)	54.7	55.2	Keeled	Yes	Double	6	14	0	9
	47–57	47–61	—	—	—	0–12	13–16	—	8–10
<i>aktites</i> (39)	54.2	57.3	Keeled	No	Yes	15	18	0	4
	47–61	44–58	—	—	—	0–22	14–20	0–7	0–7
<i>nanus</i> (2)	37	45	Keeled	No	No	3.5	14.5	0	12
	—	—	—	—	—	2–5	14–15	—	—
<i>intrudusus</i> (8)	59.2	58.4	Smooth	No	No	10	14.5	0	10
	53–65	55–65	—	—	—	2–20	14–15	—	9–11
<i>robertfisheri</i> (106)	61.1	58.3	Keeled	Yes	Yes	14	16	0	8
	50–70	48–67	—	—	—	2–24	14–19	0–1	0–12
<i>multicarinatus</i> (135)	~52.5	~52.5	Keeled	Yes	Yes	>10	18	0	8
	42–63	42–62	—	—	—	—	16–18	0–9	6–10
<i>kamiali</i> (15)	67.3	66.8	Keeled	Yes	Yes	14	19	0	9
	61–73	60–70	—	—	—	2–19	17–20	—	8–11
<i>panaeati</i> (3)	48	47.5	Keeled	Yes	Yes	17	15	0	7
	—	44–50	—	—	—	15–17	15–17	—	7–8
<i>fredkrausi</i> (19)	67.6	66.1	Keeled	Yes	Yes	14	18	3	5
	57–77	52–74	—	—	—	8–22	16–19	0–6	4–7
<i>modicus</i> (33)	58.7	56.5	Variable	Yes	Yes	24	10	3	11
	46–65	48–68	—	—	—	10–28	7–12	0–12	10–14
<i>amplus</i> (7)	78.1	67.9	Smooth	Yes	Yes	12	17	0	14
	75–82	—	—	—	—	6–24	14–20	0–11	14
<i>chrisaustini</i> (7)	41.9	37.8	Smooth	No	No	17	13	0	5
	40–45	31–43	—	—	—	14–24	12–15	0	5–7
<i>notios</i> (22)	63.9	60.0	Double	Yes	Yes	14	18	0	13
	55–71	52–70	—	—	—	12–24	13–19	0	10–15
<i>erugatus</i> (6)	69.7	63.1	Smooth	Yes	Yes	14	16.5	9	12.5
	66–72	59–69	—	—	—	10–20	15–18	6–12	12–14
<i>alotau</i> (96)	58.0	55.5	Keeled	Yes	Yes	14	12	0	8
	44–67	43–66	—	—	—	6–22	6–20	0–9	0–13
<i>heteronotus</i> (39)	43.3	42.1	Keeled	Yes	Yes	12	13	0	5
	39–47	37–48	—	—	—	6–20	11–14	0–1	0–7
<i>papua</i> (45)	57.8	59.2	Keeled	Yes	Yes	13	14	6	7
	49–64	55–64	—	—	—	0–18	11–17	0–11	0–12
<i>imundatus</i> (27)	50.9	50.7	Keeled	No	No	0	13	9	14
	48–58	45–54	—	—	—	0–10	11–15	0–13	9–15
<i>undulatus</i> (1)	—	37	Smooth	No	No	0	12	—	10

lengths $4 > 3 > 5 \approx 2 > 1$; 19 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as short row of enlarged scales.

Coloration in life unknown. In alcohol, background tan dorsally and ventrally. Top of head with scattered, irregular medium-brown marks, supra- and infralabial scales tan centered, cream edged; brown postorbital stripe from top of orbit to end of temporal area, bordered below by faded cream stripe and then brown stripe to ear opening. Dorsally from base of neck to inguinal area, 5 brown, posterior-pointed chevron marks, each with cream posterior edge. Dorsally, base of tail with bold dark and light chevron, followed by series of brown dorsal chevrons without light borders. Venter uniform light tan from chin onto tail.

ETYMOLOGY. The specific name *arceo* is Latin for “prevent access to” or “guard.” It is proposed to honor the women and men of the World War II Allied forces who fought and freed New Guinea and the Lesser Sundas from tyranny. It is proposed as a noun in apposition.

VARIATION. The only other Morotai specimen is a 29.7 mm SVL unsexed juvenile. It matches or approaches (within 1 or 2 scales) the holotype in most traits, except for a larger postmental (12). In spite of being a juvenile, its body proportions are also similar (within 2%) or identical to the adult. The presence or absence of precloacal pores in adult males is unknown.

In coloration, the juvenile is less boldly patterned, although it displays the dark-brown, white-edged chevrons from the neck onto the base of the tail.

DISTRIBUTION. Indonesia, Maluku Islands, Morotai (sample 1). Presently known only from the two specimens collected in 1944 by a U.S. soldier on active duty. The specimens were given to the BYU collections with no further collecting data other than island of origin (Figure 12).

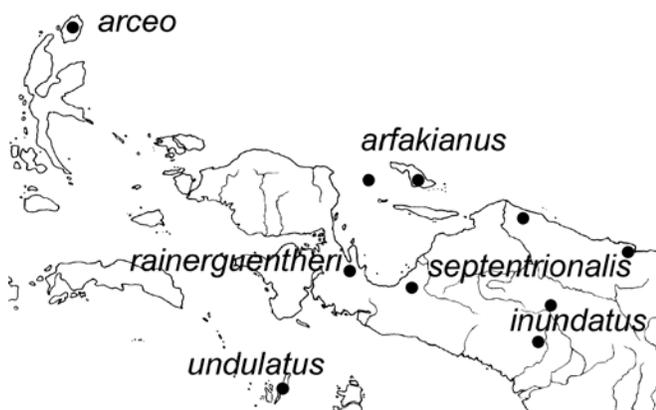


FIGURE 12. Occurrence of *Nactus* species in western New Guinea and associated islands. The solid circles are sample localities identified in Figure 1.

Nactus arfakianus (Meyer)

Arafak Slender-toed Gecko

Gymnodactylus (*Heteronota*) *arfakianus* Meyer, 1874:44 [type locality: “Neu-Guinea”; subsequently, Meyer (1887) identified the locality as Doré, a town on the northeastern coast of Pulau Yapen (=Kepulauan Yapen)].

COMMENTS. As noted in the Taxonomic Decisions section, the type was destroyed during the Dresden firebombing in February 1945. I have not designated a neotype of *Gymnodactylus arfakianus* Meyer because I have not located any specimens from Doré or Yapen. Although Palau Yapen was likely continuous with the New Guinea mainland during the last glacial epoch and recent collected specimens are available from northern coastal New Guinea, I am reluctant to designate one of the latter as a neotype. A neotype should derive from the locality of the original type specimen or very near that locality to reduce the possibility of incorrect assignment. I am, nevertheless, recognizing two individuals as representing the taxon *Nactus arfakianus* (Meyer). Both (BPBM 3951, Biak Island; UMMZ 122449, Numfoor Island) are from the Schouten Islands, of which Yapen is a member. The following data derive from these two individuals.

DEFINITION. A bisexual taxon of geckos (Gekkoniinae) of moderate adults (47–52 mm SVL) with keeled subcaudals, moderate to large postmental scales (12–21), no postmental-infralabial (PmLab) contact, moderate number of dorsal tubercle rows (15–18) and moderate number of tubercles (29–34) in parasagittal row (TubRow), tubercles on dorsal surface of thigh and crus, and 15 precloacal pores in a female (Figure 13). Diagnostic summary in Table 8.

Coloration in life is unknown. In alcohol, dorsal background medium-dark brown with series of paired dark-brown spots/blotches extending from anterior neck onto base of tail; head medium-dark brown with light-brown edging of supra- and infralabials; venter from chin to base of tail uniform brown

ETYMOLOGY. “Arfak” derives from the language of the coastal Biak people of the Vogelkop Peninsula and appears to be used for their lowland area (“inferior”) relative to the adjacent Arfak Mountains, the highest mountains on the Vogelkop. Apparently, Meyer used Arfak in a broader geographic sense to label the entire region.

DISTRIBUTION. Schouten Islands in the mouth of Cenderawasih Bay, Papua Indonesia (samples 2 and 3).

Nactus rainerguentheri, new species

Vogelkop Slender-toed Gecko

HOLOTYPE. ZMB 62760, an adult female from near Maja Brook, 550 m above sea level (asl), Wondiwoi Mountains, base of Wandammen Peninsula, 2°57'32"S 134°37'58"E, west

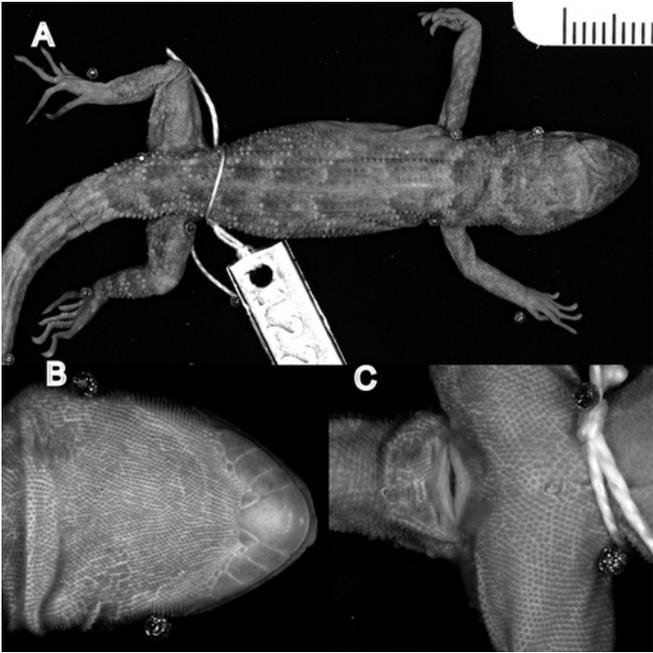


FIGURE 13. An individual of *Nactus arfakianus* from Numfoor Island (UMMZ 122449), Schouten (Biak) Islands, Papua Indonesia. (A) Dorsal view of entire body, (B) ventral view of head, and (C) ventral view of pelvis and thigh. (Photographs by E. Langan, USNM.)

of Yeretuar, Papua Indonesia, collected by Rainer Günther on 7 May 2000 (Figure 14).

PARATYPES. None.

DEFINITION. A bisexual taxon of geckos (Gekkoniinae) of moderately small adults (47 mm SVL) with keeled subcaudals, no postmental scale, few rows (<12) of dorsal tubercles, although with a large number of tubercles (37) in parasagittal row (TubRow), no tubercles on thigh and crus, and no precloacal pores in females, unknown in males. Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult female, 47.3 mm SVL, ~52 mm tail length (posterior quarter regenerated), 19.6 mm TrunkL, 19.4 mm SnForel, 12.7 mm HeadL, 8.0 mm HeadW, 5.8 mm HeadH, 3.0 mm EyeD, 4.3 mm NarEye, 3.3 mm Interorb, 1.8 mm SnW. Body proportions: 41% TrunkL/SVL, 41% SnForel/SVL, 27% HeadL/SVL, 17% HeadW/SVL, 63% HeadW/HeadL, 6% EyeD/SVL, 24% EyeD/HeadL, 34% NarEye/HeadL, 26% Interorb/HeadL, 14% SnW/HeadL.

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal trapezoidal rostral scale posterior with cleft on midline of middorsal half and distinctly depressed on its mid-posterior half; 3 large supralabials (left and right, Suplab) and 3 infralabials (left and right, Inflab) in front of anterior edge of orbit, first supra- and infralabial largest

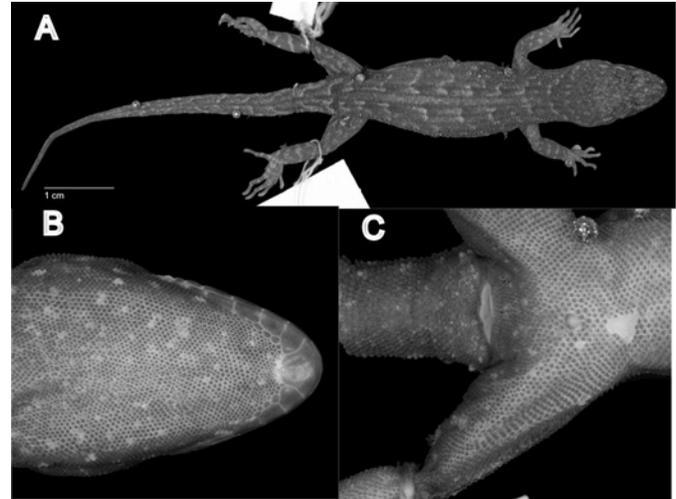


FIGURE 14. Holotype of *Nactus rainerguentheri* (ZMB 62760). (A) Dorsal view of entire body, (B) ventral view of head, and (C) ventral view of pelvis and thigh. (Photographs by E. Langan, USNM.)

of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 2 moderate-sized granular loreal scales, dorsalmost one largest. Supranasals moderate sized narrowly in contact on midline. 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 onto tail; on trunk rows reach to middle of sides, 10 entire rows (DorsTub), and only to dorsolateral edge on neck; tubercles in each row usually separated by single granular scale yielding 37 tubercles per row (TubRow); 8 rows transversely between hindlimbs (TubHip). Uniform covering of small tubercles on dorsal half of forelimb; hindlimb also with uniform small tubercles (TubHindl = 0). Tail with small uniform tubercle dorsally and laterally. Tail one quarter regenerated; ventrally with uniform, small keeled scales (Subcaud = 0). Pair of cloacal spurs (CloacS) on each side, distal edge truncate (CSTip = 0). Ventral scales from chin to vent small, uncarinate, granular, and somewhat larger on chest and abdomen. No precloacal pores. Forefoot with narrow digits, their lengths $3 > 4 \approx 2 > 5 > 1$; 15 lamellae beneath fourth digit (4FingLm), 7 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $4 \approx 3 > 5 \approx 2 > 1$; 21 lamellae beneath fourth digit (4ToeLm).

Coloration in life not reported. In alcohol, dorsal background medium brown, neck and trunk irregularly marked with narrow irregular transverse streaks of tan; sides of trunk lightly spotted in tan. Dorsally, head medium to dark brown vaguely spotted with tan, light spotting on sides of head; supra- and infralabials dark brown with sutures narrowly edged in tan and tan spots in temporal extending onto chin and throat.

Venter unicolor medium brown. Limbs dorsally with irregular tan markings. Tail brown streaked or mottled with tan.

ETYMOLOGY. The specific name honors Rainer Günther for his exemplary research into the biology and systematics of New Guinea anurans and for the discovery of this species.

VARIATION. Unknown; taxon presently known from a single individual.

DISTRIBUTION. Currently known only from the type locality (sample 4) but expected to occur in forested habitats throughout the Vogelkop.

Nactus septentrionalis, new species

North Coast Papuan Slender-toed Gecko

HOLOTYPE. USNM 119240, adult male from Netherlands New Guinea [=West Papua], Toem, opposite Wakde Island [-2.000° 139.0167°], collected by William M. Stickel on 15 June 1944 (Figure 15).

PARATYPES. MCZ R49264, adult male; MCZ R49265, immature female; MCZ R49266, adult male; MCZ R49267–268, adult females, all from Toem, Netherlands New Guinea, collected by William H. Stickel on 1 July 1944; USNM 119239, with same locality data as holotype.

DEFINITION. A bisexual taxon of geckos (Gekkoniinae) of moderate adults (♀♀ 42–54 mm, ♂♂ 42–57 mm SVL) with keeled subcaudals, variable-sized postmental scales (2–18, usually ≤ 12), no or slight postmental-infralabial (PmLab) contact,

low to moderate number of dorsal tubercle rows (12–17) and moderate number of tubercles (24–39, usually ≥ 32) in parasagittal row (TubRow), no tubercles on dorsal surface of thigh or crus, and moderate number of precloacal pores (8–12) in males (females with or without pores, 0–2). Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 46.0 mm SVL, 53 mm tail length, 19.5 mm TrunkL, 16.3 mm SnForel, 12.2 mm HeadL, 8.3 mm HeadW, 5.6 mm HeadH, 3.0 mm EyeD, 3.6 mm NarEye, 2.8 mm Interorb, 1.7 mm SnW. Body proportions: 42% TrunkL/SVL, 35% SnForel/SVL, 27% HeadL/SVL, 18% HeadW/SVL, 68% HeadW/HeadL, 7% EyeD/SVL, 25% EyeD/HeadL, 30% NarEye/HeadL, 23% Interorb/HeadL, 14% SnW/HeadL.

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal trapezoidal rostral scale posterior with cleft on midline of middorsal third and lightly depressed on its mid-posterior half; 3 large supralabials (left and right, Suplab) and 3 infralabials (left and right, Inflab) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 3 enlarged granular loreal scales, dorsalmost one largest. Supranasals moderate sized broadly in contact on midline. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large trapezoidal mental and modest postmentals (Postm = 10). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach to middle of sides, 12 entire rows (DorsTub), and only to dorsolateral edge on neck; tubercles in each row usually separated by 1 or 2 granular scales, yielding 34 tubercles per row (TubRow); 10 rows transversely between hindlimbs (TubHip). Uniform covering of small tubercles on dorsal half of forelimb; hindlimb also with uniform small tubercles (TubHindl = 0). Tail with small uniform tubercle dorsally and laterally. Tail entire; ventrally with uniform, small keeled scales (Subcaud = 0). Pair of cloacal spurs (CloacS) on each side, distal edge truncate (CSTip = 0). Ventral scales from chin to vent small, granular, and somewhat larger on chest and abdomen. Precloacal pores 12. Forefoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 16 lamellae beneath fourth digit (4FingLm), 5 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $4 \approx 3 > 2 \approx 5 > 1$; 20 lamellae beneath fourth digit (4ToeLm).

In alcohol, brown ground color dorsally from head to tail tip with small, dark-brown irregular markings on head, modest-sized spots scattered across dorsum and hindlimbs, forelimbs uniform brown, dark-brown chevron edged posteriorly by beige at base of tail, remainder of tail mottled with dark brown; face (loreal) with irregular dark-brown preorbital stripe broadly bordered above and below by beige, similar narrow dark-brown postorbital stripe edged by beige. Venter from chin to vent uniform brown, same for underside of limbs; chin and anterior throat with light-brown spots.

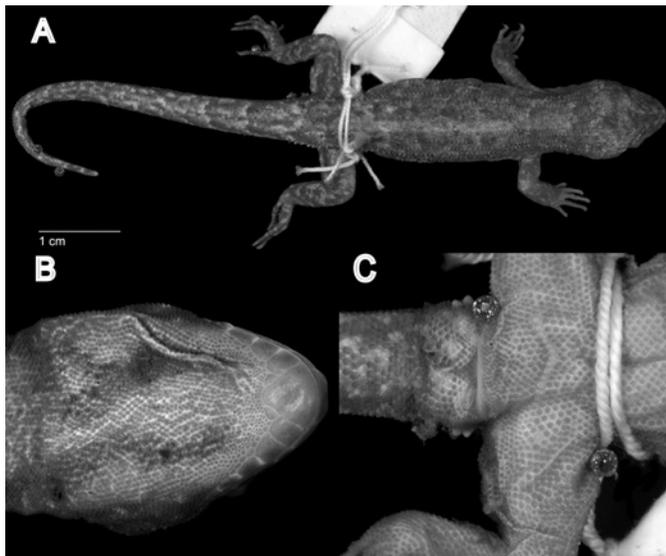


FIGURE 15. Holotype of *Nactus septentrionalis* (USNM 119240). (A) Dorsal view of entire body, (B) ventral view of head, and (C) ventral view of pelvis and thigh. (Photographs by E. Langan, USNM.)

ETYMOLOGY. The specific name *septentrionalis* is Latin for “north” or “northerly.” It is proposed to designate the occurrence of this species along the north coast of New Guinea. It is proposed as an adjective.

VARIATION. Females and males display no metric differences (adult ♀♀ 49.1, 42.2–53.9 mm [mean and range, respectively, throughout]; adult ♂♂ 48.7, 41.6–56.6 mm SVL) and also share proportions (total adult sample): TrunkL/SVL 40.8%, 32%–48%; HeadL/SVL 26.8%, 25%–29%; HeadW/SVL 18.1%, 16%–20%; HeadW/HeadL 67.4%, 58%–75%; EyeD/SVL 6.6%, 6%–8%; EyeD/HeadL 25%, 21%–31%; NarEye/HeadL 31.1%, 27%–34%; Interorb/HeadL 27.5%, 22%–33%; SnW/HeadL 15.2%, 10%–20%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; large supralabials (4, 3–4 [median and range, respectively, throughout]) and infralabials (3, 3–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and small to modest postmentals (Postm = 6, 2–8) and usually no genial scale between postmental and first surpalabial (0, 0–1 PmLab); dorsally, trunk with 14, 12–17 (DorsTub) enlarged tubercles transversely on dorsum and with 35, 24–40 tubercles (TubRow) longitudinally along trunk; 9, 6–10 tubercle rows transversely between hindlimbs (TubHip). Uniform covering of small tuberculate-like scale on dorsal half of forelimb and hindlimb and no enlarged tubercles (TubHindl = 0). Tail with small uniform scales dorsally and laterally, ventrally with uniform, small keeled scales (Subcaud = 0). Usually, pair of cloacal spurs (2, 1–2 CloacS) on each side. Ventral scales from chin to vent small, tuberculate, granular, somewhat larger on chest and abdomen. Preloacal pores, males 8–12, females 0–9. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 \approx 5 > 1$; 16, 14–20 lamellae beneath fourth digit (4FingLm), 6, 4–8 scale rows on palm; hindfoot with narrow digits, their lengths $4 \approx 3 > 2 \approx 5 > 1$; 21, 20–24 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, not observed to be strikingly different than for the holotype.

DISTRIBUTION. North coast of New Guinea from Nabire, Papua Indonesia, to East Sepik Province, Papua New Guinea (samples 5, 6, 7, 8, 9, 10, 11, 12, and 13). In Wewak and Sepik River–Ambunti area, it is sympatric with *N. allenallisoni*.

***Nactus allenallisoni*, new species**

Madang Slender-toed Gecko

HOLOTYPE. AMS R31261, adult male from Papua New Guinea, Madang Province, Siar Plantation [–5.1917° 145.7774°], Alexishafen, collected by S. Donnellan on 19 March 1987 (Figure 16).

PARATYPES. AMNH 104874, adult male from Wanuma, Adelbert Mountains [–4.9195° 145.3182°], Madang Province, collected by R. G. Zweifel on 4 August 1969; AMNH

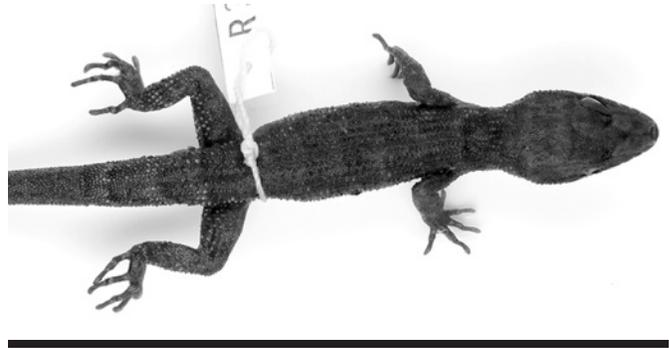


FIGURE 16. Holotype of *Nactus allenallisoni* (AMS R31261). Dorsal view of entire body. (Photograph by S. Mahony, AMS.)

104873, adult female, vicinity of Sempì [–5.1486° 145.7715°], ca. 5 miles [~8 km] N of Alexishafen, Madang Province collected by R. G. Zweifel on 13 July 1969; AMS R31260, R31262, R31268, R31281, adult males with same collecting data as holotype; AMS R31272, R31284, R31291, R31297, adult females with same collecting data as holotype.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with moderate to large adults (♀♀ 47–64 mm, ♂♂ 46–63 mm SVL) with keeled subcaudals, variable-sized postmental scales (0–22, median 14), no or slight postmental-infralabial (PmLab) contact, low to moderate number of dorsal tubercle rows (12–22) and moderate number of tubercles (22–36, usually ≥ 28) in parasagittal row (TubRow), tubercles on dorsal surface of thigh and crus, and few preloacal pores (2, 0–9) in males (most females without pores, 0–3). Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 55.0 mm SVL, tail length not recorded, 18.4 mm TrunkL, 23.4 mm SnForel, 15.3 mm HeadL, 10.1 mm HeadW, 7.3 mm HeadH, 3.6 mm EyeD, 4.9 mm NarEye, 4.5 mm Interorb, 2.2 mm SnW. Body proportions: 34% TrunkL/SVL, 42% SnForel/SVL, 28% HeadL/SVL, 18% HeadW/SVL, 65% HeadW/HeadL, 7% EyeD/SVL, 24% EyeD/HeadL, 32% NarEye/HeadL, 29% Interorb/HeadL, 14% SnW/HeadL.

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal trapezoidal rostral scale posterior with cleft on midline of middorsal third and lightly depressed on its mid-posterior half; 3 large supralabials (right) and 3 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 3 enlarged granular loreal scales, dorsalmost one largest. Supranasals moderate sized in contact on midline. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large trapezoidal mental and modest postmentals (Postm = 14) touching first supralabial (PmLab = 0). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach to middle of sides, 16 entire

rows (DorsTub); tubercles in each row usually separated by more than 1 granular scale, yielding 29 tubercles per row (TubRow); 9 rows transversely between hindlimbs (TubHip). Some enlarged tubercles on dorsal surface of forelimb; hindlimb also with enlarged tubercles (TubHindl = 2) on dorsal surface of thigh and crus. Tail with small uniform scales dorsally and laterally; ventrally with uniform, small keeled scales (Subcaud = 0). Single cloacal spur (CloacS) on each side, distal edge truncate (CSTip = 0). Ventral scales from chin to vent small, granular and somewhat larger on chest and abdomen. Preloacal pores 3. Forefoot with narrow digits; 17 lamellae beneath fourth digit (4FingLm), 4 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, 21 lamellae beneath fourth digit (4ToeLm).

Coloration in life unknown. In alcohol, background rufous tan dorsally and lighter ventrally. Top of head with scattered, smudge-like medium-brown marks. Dorsally dark brown, parasagittal smudge-like marks on middle of neck, 5 pairs of parasagittal dark-brown blotches on trunk and 1 on base of tail. Limbs with scattered diffuse dark marks.

ETYMOLOGY. This species is named to recognize Allen Allison's contributions to the biology of the New Guinea herpetofauna and his continuing role in the conservation of the Papua New Guinea biota by encouraging and supporting the active involvement of PNG villagers and tribes. The specific name is a noun in apposition.

VARIATION. Females and males display no striking metric differences (adult ♀♀ 56.6, 47.0–64.3 mm; adult ♂♂ 53.2, 45.9–62.5 mm SVL) and also share proportions (total adult sample) TrunkL/SVL 39.8%, 32%–46%; HeadL/SVL 27.4%, 25%–40%; HeadW/SVL 18.1%, 15%–22%; HeadW/HeadL 65.9%, 48%–75%; EyeD/SVL 6.7%, 5%–9%; EyeD/HeadL 24%, 19%–33%; NarEye/HeadL 32.2%, 21%–43%; Interorb/HeadL 27.1%, 21%–32%; SnW/HeadL 14.5%, 9%–18%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; large supralabials (3, 3–4) and infralabials (3, 3–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and usually modest to large postmentals (Postm = 14, 0–22, single specimen lacking postmental) and usually no genial scale between postmental and first surpalabial (0, 0–3 PmLab); dorsally, trunk with 17, 12–22 (DorsTub) enlarged tubercles transversely on dorsum and with 29, 22–36 tubercles (TubRow) longitudinally along trunk; 10, 8–10 tubercle rows transversely between hindlimbs (TubHip). Scattering of large tubercles on dorsal half of forelimb and more on hindlimb (TubHindl = 2). Tail with small uniform scales dorsally and laterally, ventrally with uniform, small keeled scales (Subcaud = 0, with exception of one individual with smooth subcaudals). Usually, 1 cloacal spur (1, 0–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Preloacal pores, males 0–9, females 0–3. Forefoot with narrow digits,

their lengths usually $3 > 4 \approx 2 > 5 \approx 1$; 17, 15–20 lamellae beneath fourth digit (4FingLm), 5, 4–7 scale rows on palm; hindfoot with narrow digits, their lengths $4 \approx 3 > 5 > 2 > 1$; 22, 19–25 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, dorsal background medium brown from snout onto tail, ill-defined interorbital dark-brown mark extending narrowly onto snout, dark-brown reverse triangular mark on parietal-crown, and series of paired parasagittal dark-brown marks from nape onto base of tail; brown of dorsum grading into lighter brown of venter, uniform from chin onto base of tail.

DISTRIBUTION. North coast Papua New Guinea from Aitape eastward to Guisko and Finschhafen of coastal Huon Peninsula and also on Manam and Karkar Islands (samples 11, 12, 15, 16, 17, 18, 20, 23, 24). *Nactus allenallisoni* is sympatric with *N. septentrionalis* in Aitape, Nuku, Wewak, and Manam Island and with *N. nanus* at Siar Plantation; it has not been reported from the coastal areas of eastern Madang and western Morobe provinces.

The Alexishafen specimens (Amron and Pig Island, CAS 192884, 192887–88, 192903) of Zug and Fisher (2012) are morphologically *N. allenallisoni*; however, CAS 192884 shows a closer genetic relationship to another lineage of Madang area bisexuals (Zug and Fisher, 2012: fig. 3). Does this relationship indicate it is a hybrid of one of the two other synoptic species of this area? Donnellan and Moritz (1995) reported AMS R124028 as a hybrid; morphologically, it is *N. allenallisoni*.

Nactus grevifer, new species

Torricelli Slender-toed Gecko

HOLOTYPE. IRSNB 15802Q, adult male from Papua New Guinea, West Sepik Province, Kumnatei [–3.45° 142.12°], collected by Benoit Mys in early 1980s.

PARATYPES. IRSNB 15802A–F, adult females with the same collecting data as the holotype, and IRSNB 15802K–N, adult males with the same collecting data as the holotype.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with moderate adults (♀♀ 47–57 mm, ♂♂ 47–61 mm SVL) with keeled subcaudals, no to small postmental scales (0–12, median 6), no or slight postmental-infralabial (0–2) contact, moderate number of dorsal tubercle rows (13–16), and moderately high number of tubercles (31–39) in parasagittal row (TubRow), strongly tuberculate dorsal surface of thigh and crus (large tubercles forming sheath-like surface), and modest number of preloacal pores (8–11) in males (females without pores). Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 55.1 mm SVL, tail length not recorded, 21.1 mm TrunkL, 21.9 mm SnForel, 13.9 mm HeadL, 9.2 mm HeadW, 6.8 mm HeadH, 2.5 mm EyeD, 4.2 mm NarEye, 2.7 mm Interorb, 1.9 mm SnW. Body proportions: 39% TrunkL/SVL, 42% SnForel/SVL, 28% HeadL/SVL, 19% HeadW/SVL, 66% HeadW/HeadL,

7% EyeD/SVL, 19% EyeD/HeadL, 30% NarEye/HeadL, 20% Interorb/HeadL, 12% SnW/HeadL.

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal trapezoidal rostral scale posterior with cleft on midline of middorsal third and lightly depressed on its mid-posterior half; 4 large supralabials (right) and 3 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 3 enlarged granular loreal scales, dorsalmost one largest. Supranasals moderate sized in contact on midline. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large trapezoidal mental and small postmentals (Postm = 4) separated from first supralabial (PmLab = 1). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach to middle of sides, 14 entire rows (DorsTub); tubercles in each row usually separated by 1 granular scale, yielding 34 tubercles per row (TubRow); 10 rows transversely between hindlimbs (TubHip). Some enlarged tubercles on dorsal surface of forelimb; hindlimb sheathed with enlarged tubercles (TubHindl = 3) on dorsal surface of thigh and crus. Tail with small uniform scales dorsally and laterally; ventrally with uniform, small keeled scales (Subcaud = 0). Single cloacal spur (CloacS) on each side, distal edge pointed (CSTip = 1). Ventral scales from chin to vent small, granular and somewhat larger on chest and abdomen; precloacal pores 8. Forefoot with narrow digits; 18 lamellae beneath fourth digit (4FingLm), 5 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, 22 lamellae beneath fourth digit (4ToeLm).

In life, coloration has not been reported; in alcohol it was not recorded.

ETYMOLOGY. Specific name derives from the impression of leg armor by the heavily tuberculate outer surface of the hindlimbs, hence wearing leg armor, that is, greaves. "Greave" derives from the Old French *greve* for leg armor. The Latin *fero* refers to "carrying," and its suffix is *ifer*, hence *grevifer*, or wearer of leg armor. The specific name is a noun in apposition.

VARIATION. Females and males from Kumnatei (locality 38, $n = 17$) display no striking metric differences (adult ♀♀ 54.7, 51.8–57.1 mm; adult ♂♂ 55.2, 51.8–61.1 mm SVL) and also share similar proportions (total Kumnatei adult sample): TrunkL/SVL 42.2%, 37%–49%; HeadL/SVL 26.3%, 25%–29%; HeadW/SVL 18.1%, 16%–17%; HeadW/HeadL 69.3%, 64%–74%; EyeD/SVL 5.2%, 5%–6%; EyeD/HeadL 20.1%, 18%–23%; NarEye/HeadL 31.0%, 30%–32%; Interorb/HeadL 22.3%, 17%–28%; SnW/HeadL 13.4%, 11%–15%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; large supralabials (3, 3–4) and infralabials (3, 2–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and no to small postmentals (Postm = 4, 0–10, single specimen lacking postmental) and usually no genial

scale between postmental and first supralabial (0, 0–2 PmLab); dorsally, trunk with 14, 13–16 (DorsTub) enlarged tubercles transversely on dorsum and with 35, 33–39 tubercles (TubRow) longitudinally along trunk; 10, 8–11 tubercle rows transversely between hindlimbs (TubHip). Scattering of large tubercles on dorsal half of forelimb and sheath of tubercles on hindlimb (TubHindl = 3). Tail with small uniform scales dorsally and laterally, ventrally with uniform, small keeled scales (Subcaud = 0 with exception of one individual with smooth subcaudals). Usually, 2 cloacal spurs (2, 1–3 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 8–10, females 0. Forefoot with narrow digits, their lengths usually $3 > 4 \approx 2 > 5 \approx 1$; 17, 16–19 lamellae beneath fourth digit (4FingLm), 6, 5–8 scale rows on palm; hindfoot with narrow digits, their lengths $4 \approx 3 > 5 > 2 > 1$; 22, 19–24 lamellae beneath fourth toe (4ToeLm).

A distant sample (locality = 21) from the Bom area contains individuals identified as *N. allenallisoni* ($n = 2$) and *N. grevifer* ($n = 5$). In spite of the distance from the *grevifer* type locality, I treat the latter specimens as that species. They are somewhat smaller (adult ♀♀ 54.7, 51.8–57.1 mm; adult ♂♂ 55.2, 51.8–61.1 mm SVL) and also share proportional differences (total Kumnatei adult sample): TrunkL/SVL 42.2%, 37%–49%; HeadL/SVL 26.3%, 25%–29%; HeadW/SVL 18.1%, 16%–17%; HeadW/HeadL 69.3%, 64%–74%; EyeD/SVL 5.2%, 5%–6%; EyeD/HeadL 20.1%, 18%–23%; NarEye/HeadL 31.0%, 30%–32%; Interorb/HeadL 22.3%, 17%–28%; SnW/HeadL 13.4%, 11%–15%. They also possess some differences in scalation. Large supralabials (3, 3–3) and infralabials (3, 2–3) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and small to medium postmentals (Postm = 8, 6–12) and usually no genial scale between postmental and first supralabial (0, 0–1 PmLab); dorsally, trunk with 14, 13–15 (DorsTub) enlarged tubercles transversely on dorsum and with 29, 25–30 tubercles (TubRow) longitudinally along trunk; 8, 7–8 tubercle rows transversely between hindlimbs (TubHip). Scattering of large tubercles on dorsal half of forelimb and sheath of tubercles on hindlimb (TubHindl = 3). Tail with small uniform scales dorsally and laterally, ventrally with uniform, small keeled scales (Subcaud = 0, with exception of one individual with smooth subcaudals). Usually, 2 cloacal spurs (2, 1–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, females 0; the single male has 8 precloacal pores and a single femoral pore on each side. Forefoot with narrow digits, with 14, 13–15 lamellae beneath fourth digit (4FingLm), 5, 5–6 scale rows on palm; hindfoot with narrow digits, 18, 16–20 lamellae beneath fourth toe (4ToeLm).

DISTRIBUTION. In the north coast Torricelli mountain range of Papua New Guinea, East Sepik Province, Kumnatei (IRSNB 15802A–S; sample 10). A distant population (IRSNB 15871.13844–845, 15871.13847, 15871.1373, 15871.1379) in the Bom area (sample 21) of Madang has a *grevifer*-style hindlimb morphology and is tentatively included in this species.

***Nactus aktites*, new species**
Madang Coastal Slender-toed Gecko

HOLOTYPE. IRSNB 15875.1516, adult male from Papua New Guinea, Madang Province, Awar [14.1362° 144.8664°], collected by Benoit Mys in early 1980s.

PARATYPES. IRSNB 15875.1500, 15875.1570, 15875.1618, 15875.1649, adult males, and IRSNB 15875.1526, 15875.1547, 15875.1569, 15875.1621, adult females with the same collection data as the holotype.

DEFINITION. A bisexual taxon of geckos (Gekkoniinae) with moderate adults (♀♀ 49–61 mm, ♂♂ 44–58 mm SVL) with keeled subcaudals, large postmental scales (median 15), no or slight postmental-infralabial (0–2) contact, moderate number of dorsal tubercle rows (14–20) and moderately high number of tubercles (26–33) in parasagittal row (TubRow), enlarged tubercle only on dorsal surface of crus, and no or few precloacal pores (0–7) in males and usually none in females. Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 52.9 mm SVL, tail length not recorded, 18.8 mm TrunkL, 22.0 mm SnForel, 15.8 mm HeadL, 11.1 mm HeadW, 7.4 mm HeadH, 3.1 mm EyeD, 4.8 mm NarEye, 3.9 mm Interorb, 1.9 mm SnW. Body proportions: 36% TrunkL/SVL, 42% SnForel/SVL, 30% HeadL/SVL, 21% HeadW/SVL, 70% HeadW/HeadL, 6% EyeD/SVL, 20% EyeD/HeadL, 30% NarEye/HeadL, 25% Interorb/HeadL, 12% SnW/HeadL.

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal trapezoidal rostral scale posterior with cleft on midline of middorsal third and lightly depressed on its mid-posterior half; 3 large supralabials (right) and 3 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 3 enlarged granular loreal scales, dorsalmost one largest. Supranasals moderate sized. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large trapezoidal mental and large postmentals (Postm = 18) touching first supralabial (PmLab = 0). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach to middle of sides, 19 entire rows (DorsTub); tubercles in each row usually separated by 1 or 2 granular scales, yielding 27 tubercles per row (TubRow); 8 rows transversely between hindlimbs (TubHip). Few scattered enlarged tubercles on dorsal surface of forelimb; hindlimb with enlarged tubercles only on dorsal surface of crus (TubHindl = 1). Tail with small uniform scales dorsally and laterally; ventrally with uniform, small keeled scales (Subcaud = 0). Single cloacal spur (CloacS) on each side, distal edge pointed (CSTip = 1). Ventral scales from chin to vent small, granular and somewhat larger on chest and abdomen. Precloacal pores 5. Forefoot with narrow digits; 17 lamellae beneath fourth digit (4FingLm), 5 scale rows between lamellae at base

of first and fifth fingers (Palm). Hindfoot with narrow digits, 21 lamellae beneath fourth digit (4ToeLm).

ETYMOLOGY. The Greek *aktites* is a masculine noun for a shore or coast dweller. The name reflects this species' presence on coastal islands and coastal lowlands of Madang and East Sepik Provinces. The specific name is a noun in apposition.

VARIATION. Females and males display slight metric differences (adult ♀♀ 54.2, 46.8–60.8 mm; adult ♂♂ 51.3, 43.8–58.0 mm SVL) and share similar proportions (total adult sample): TrunkL/SVL 39.5%, 35%–45%; HeadL/SVL 27.6%, 23%–30; HeadW/SVL 19.6%, 16%–22%; HeadW/HeadL 71.1%, 60%–80%; EyeD/SVL 6.0%, 5%–8%; EyeD/HeadL 21.7%, 18%–27%; NarEye/HeadL 31.3%, 28%–37%; Interorb/HeadL 24.9%, 17%–33%; SnW/HeadL 13.5%, 12%–16%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; large supralabials (3, 3–4) and infralabials (3, 2–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and usually moderately large postmentals (Postm = 15, 0–22) and usually no genial scale between postmental and first supralabial (0, 0–2 PmLab); dorsally, trunk with 18, 14–20 (DorsTub) enlarged tubercles transversely on dorsum and with 29, 26–33 tubercles (TubRow) longitudinally along trunk; 10, 8–11 tubercle rows transversely between hindlimbs (TubHip). Uniform covering of small tuberculate-like scale on dorsal half of forelimb and tubercles only on crus (TubHindl = 1). Tail with small uniform scales dorsally and laterally, ventrally with uniform, small keeled scales (Subcaud = 0). Usually, single cloacal spurs (1, 1–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 0–7, median 4; females 0–7, median 0. Forefoot with narrow digits, their lengths usually 3≈4>2≈5>1; 17, 14–20 lamellae beneath fourth digit (4FingLm), 5, 4–6 scale rows on palm; hindfoot with narrow digits, their lengths 4≈3>2≈5>1; 21, 19–20 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, not recorded.

DISTRIBUTION. *Nactus aktites* occurs on the north coast of Papua New Guinea from Wewak, East Sepik Province, to Alexishafen, Madang Province (samples 14, 15, 16, 18, 21). It occurs in sympatry in northwest Madang Province, Manam Island, the Alexishafen area, and Bom with *N. allenallisoni*.

***Nactus nanus*, new species**
Dwarf North-coast Slender-toed Gecko

HOLOTYPE. AMS R124053, adult male from Papua New Guinea, Madang Province, Siar Plantation near Alexishafen [–5.1667° 145.7500°], collected by S. Donnellan on 19 March 1987 (Figure 17).

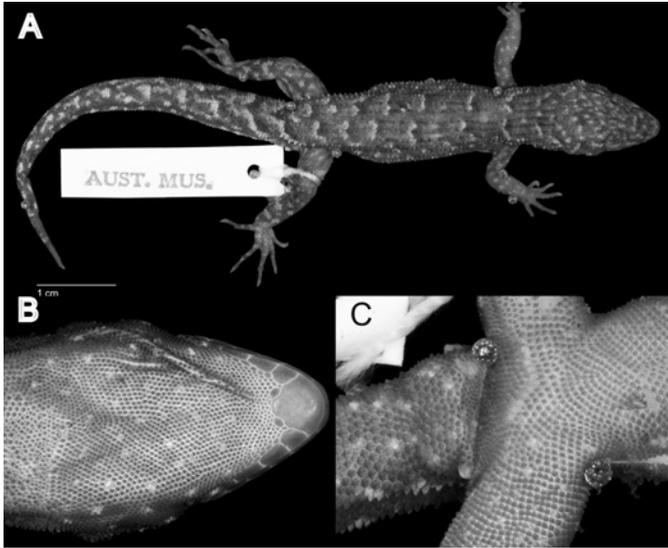


FIGURE 17. Holotype of *Nactus nanus* (AMS R124053). (A) Dorsal view of entire body, (B) ventral view of head, and (C) ventral view of pelvis and thigh. (Photographs by E. Langan, USNM.)

PARATYPES. AMS R124051, adult female with same collecting data as holotype.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) of small adults (37–45 mm SVL) with keeled subcaudals, small to moderate postmental scales (2–5), no or slight postmental-infralabial (PmLab) contact, low to moderate number of dorsal tubercle rows (14–15) and moderate number of tubercles (33–34) in parasagittal row (TubRow), high number of precloacal pores (12) in males, none in females. Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 44.8 mm SVL, tail length not recorded, 18.2 mm TrunkL, 18.4 mm SnForel, 11.5 mm HeadL, 8.1 mm HeadW, 5.8 mm HeadH, 2.7 mm EyeD, 3.7 mm NarEye, 3.3 mm Interorb, 1.8 mm SnW. Body proportions: 41% TrunkL/SVL, 41% SnForel/SVL, 26% HeadL/SVL, 18% HeadW/SVL, 70% HeadW/HeadL, 6% EyeD/SVL, 24% EyeD/HeadL, 32% NarEye/HeadL, 29% Interorb/HeadL, 16% SnW/HeadL.

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal trapezoidal rostral scale posterior with cleft on midline of middorsal third and lightly depressed on its mid-posterior half; 3 large supralabials (right) and 2 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 3 enlarged granular loreal scales, dorsalmost one largest. Supranasals moderate sized. Scales on outer edge

of eyelid slightly enlarged, forming low crenate border. Chin with moderately large trapezoidal mental and large postmentals (Postm = 15) separated from first supralabial by 1 genial scale (PmLab = 1). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach to middle of sides, 15 entire rows (DorsTub); tubercles in each row usually separated by 1 or 2 granular scales, yielding 33 tubercles per row (TubRow); 8 rows transversely between hindlimbs (TubHip). No enlarged tubercles on dorsal surface of forelimb and hindlimb (TubHindl = 0). Tail with small uniform scales dorsally and laterally; ventrally with uniform, small keeled scales (Subcaud = 0). Single cloacal spur (CloacS) on each side, distal edge blunt (CSTip = 0). Ventral scales from chin to vent small, granular, and somewhat larger on chest and abdomen. Precloacal pores 12. Forefoot with narrow digits; 11 lamellae beneath fourth digit (4FingLm), 5 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, 19 lamellae beneath fourth digit (4ToeLm).

Coloration in life not known. In alcohol, background medium brown dorsally and laterally, venter lighter brown; top of head spotted in white from snout to nape, neck to base of tail with paired dark-brown bars edged with white of equal size as dark bars, 6 pairs from axilla to sacrum; brown bars coalesce at base of tail, still bordered in white, after second dark bar, brown fades, and top of remainder of tail with irregularly shaped white spots; fore- and hindlimbs white spotted. Venter light brown with small white spots on chin and throat, also on pubis and onto tail.

ETYMOLOGY. This population has the smallest adults on the northern PNG coast. The Latin *nanus* is a masculine noun for dwarf and is proposed in recognition of this species' diminutive size. The specific name is a noun in apposition.

VARIATION. The female (36.8 mm SVL) is smaller than male, although with similar proportions: TrunkL/SVL 44%; HeadL/SVL 25%; HeadW/SVL 19%; HeadW/HeadL 76%; EyeD/SVL 7%; EyeD/HeadL 26%; NarEye/HeadL 34%; Interorb/HeadL 32%; SnW/HeadL 16%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; large supralabials (3) and infralabials (2) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and small postmentals (Postm = 2) and no genial scale between postmental and first supralabial (PmLab = 0); dorsally, trunk with 14 (DorsTub) enlarged tubercles transversely on dorsum and with 34 tubercles (TubRow) longitudinally along trunk; 8 tubercle rows transversely between hindlimbs (TubHip). Uniform covering of small scale on dorsal forelimb and hindlimb (TubHindl = 0). Tail with small uniform scales dorsally and laterally, ventrally with uniform, small keeled scales (Subcaud = 0). Three cloacal spurs on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal

pores, male 12, female none. Forefoot with narrow digits, their lengths usually $4 > 3 > 2 \approx 5 > 1$; 13 lamellae beneath fourth digit (4FingLm), 6 scale rows on palm; hindfoot with narrow digits, their lengths $4 > 3 \approx 5 > 2 > 1$; 19 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, as in holotype.

DISTRIBUTION. This species is known from only two specimens collected at the Siar Plantation, west of Madang, Madang Province, Papua New Guinea (sample 19), amid a large sample of *N. allenallisoni* (Figure 18).

Nactus intrudus, new species

Markham Slender-toed Gecko

HOLOTYPE. AMNH 95175, adult male from Papua New Guinea, Morobe Province, Busu River, 8 miles [~ 12.9 km] north of Lae [-6.7333° 146.9999°], collected by R. G. Zweifel and G. Sluder on 14 August 1964 (Figure 19).

PARATYPES. All from Papua New Guinea, Morobe Province. Adult females: AMNH 92664, Upper Markham Valley, Umi River (?), 475 m collected by H. M. Van Duesen on 17 November 1959; AMNH 95177, Lae [-6.7333° 146.9999°], collected by R. G. Zweifel on 17 July 1964; AMNH 103243, 7 miles [~ 11.3 km] (road) north of Lae [~ -6.6352 146.9808], collected by R. G. Zweifel on 25 August 1968. Adult male: AMNH 103242, 7 miles [~ 11.3 km] (road) north of Lae [~ -6.6352 146.9808], collected by R. G. Zweifel on 25 August 1968.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with moderate to large adults (♀♀ 53–65 mm, ♂♂ 55–65 mm SVL) with smooth subcaudals, moderate to large postmental scales (usually ≤ 10), no or slight postmental-infralabial (0–1) contact, moderate number of dorsal tubercle rows (14–15) and moderately high number of tubercles (26–36) in parasagittal row (TubRow), no enlarged tubercles on dorsal surface of hindlimb, and modest number of precloacal pores (9–11) in males and none in females. Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 63.0 mm SVL, tail length not recorded, 27.0 mm TrunkL, 26.0 mm SnForel, 16.9 mm HeadL, 11.4 mm HeadW, 7.6 mm HeadH, 4.4 mm EyeD, 5.2 mm NarEye, 5.5 mm Interorb, 2.5 mm SnW. Body proportions: 43% TrunkL/SVL, 41% SnForel/SVL, 27% HeadL/SVL, 18% HeadW/SVL, 68% HeadW/HeadL, 7% EyeD/SVL, 26% EyeD/HeadL, 31% NarEye/HeadL, 33% Interorb/HeadL, 15% SnW/HeadL.

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal trapezoidal rostral scale posterior with cleft on midline of middorsal third and lightly depressed on its mid-posterior half; 4 large supralabials (right) and 4 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales

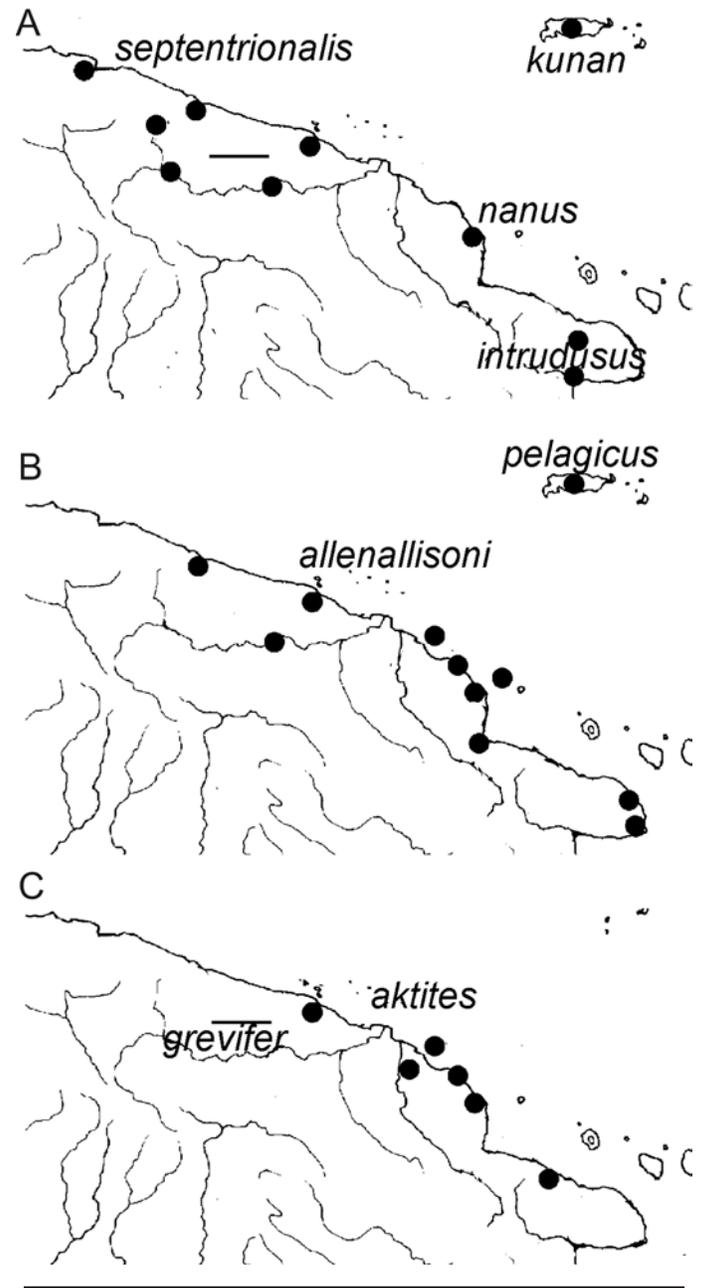


FIGURE 18. Occurrence of *Nactus* species in West Sepik Province to the Huon Peninsula and Markham Valley of Papua New Guinea. The solid circles are sample localities identified in Figure 1. (A) *Nactus septentrionalis*, *N. nanus*, and *N. intrudus* on the mainland and *N. kunan* on Manus Island. (B) *Nactus allenallisoni* on the mainland and *N. pelagicus* on Manus Island. (C) *Nactus grevifer* and *N. aktites* on the mainland.



FIGURE 19. Holotype of *Nactus intrudusus* (AMNH 95175). Dorsal view of entire body. (Photograph by L. Vonnahme, AMNH.)

and posteriorly 3 enlarged granular loreal scales, dorsalmost one largest. Supranasals moderate sized. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large trapezoidal mental and moderately large postmentals (Postm = 14) touching first supralabial (PmLab = 0). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach to middle of sides, 15 entire rows (DorsTub); tubercles in each row usually separated by 1 or 2 granular scales, yielding 27 tubercles per row (TubRow); 8 rows transversely between hindlimbs (TubHip). No enlarged tubercles on dorsal surface of forelimbs or hindlimbs (TubHindl = 0). Tail with small uniform scales dorsally and laterally; ventrally with uniform, small smooth scales (Subcaud = 1). Single cloacal spur (CloacS) on each side, distal edge rounded (CSTip = 0). Ventral scales from chin to vent small, granular and somewhat larger on chest and abdomen. Precloacal pores 9. Forefoot with narrow digits; 18 lamellae beneath fourth digit (4FingLm), 6 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, 22 lamellae beneath fourth digit (4ToeLm).

Coloration in life not reported. In alcohol, dorsally head and trunk background medium orangish brown, limbs same, tail lighter. Snout and loreals lighter brown, large dusky-brown triangle in middle of head, fading to trunk color on nape. Dorsally, from base of neck to inguinal area, 6 paired dark-brown marks from base of neck to sacrum, solid dark transverse bar on base of tail, then becoming paired dark-brown spots edged posteriorly in white thereafter.

ETYMOLOGY. This unique population seemingly intrudes between north coast populations with tuberculate limbs and keeled subcaudal scales, hence the use of the Latin *intrudo*, *intrudusus* for “intruder.” The specific name is proposed as a noun in apposition.

VARIATION. Females and males display only slight metric differences (adult ♀♀ 59.2, 52.7–65.0 mm; adult ♂♂

58.4, 55.3–63.0 mm SVL) and share similar proportions (total adult sample): TrunkL/SVL 42.0%, 36%–46%; HeadL/SVL 26.7%, 26%–27%; HeadW/SVL 17.9%, 17%–19%; HeadW/HeadL 66.9%, 62%–69%; EyeD/SVL 7.2%, 6–8%; EyeD/HeadL 27.0%, 24%–29%; NarEye/HeadL 32.1%, 31%–33%; Interorb/HeadL 32.9%, 29%–37%; SnW/HeadL 16.2%, 15–17%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; large supralabials (4, 3–4) and infralabials (4, 3–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and usually moderately large postmentals (Postm = 10, 2–20) and usually no genial scale between postmental and first supralabial (0, 0–1 PmLab); dorsally, trunk with 14, 14–15 (DorsTub) enlarged tubercles transversely on dorsum and with 29, 26–36 tubercles (TubRow) longitudinally along trunk; 8, 7–9 tubercle rows transversely between hindlimbs (TubHip). Uniform covering of small tuberculate-like scale on dorsal half of forelimb and hindlimb (TubHindl = 0). Tail with small uniform scales dorsally and laterally, ventrally with uniform, small usually smooth scales (Subcaud = 1, 0–1). Usually, single cloacal spurs (1, 1–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 9–11, females 0. Forefoot with 17, 17–18 lamellae beneath fourth digit (4FingLm), 6, 5–6 scale rows on palm; hindfoot with 20, 20–22 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, as in holotype.

DISTRIBUTION. Markham River valley in Morobe Province, Papua New Guinea. (sample 25).

Nactus kunan Fisher and Zug in Zug and Fisher, 2012

Admiralty or Bumble-bee Slender-toed Gecko

HOLOTYPE. USNM 576300, adult female from Papua New Guinea, Admiralty Islands, Manus Island, Sohoniili Village, -2.11296° 147.14912° , collected by Robert N. Fisher and villagers from Sohoniili Village, 26 May 2010.

PARATYPES. Same collection data as holotype PNGNM 25190, juvenile female.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with moderate adults (♀ 56 mm SVL) with smooth subcaudals, no postmental scales, moderate number of dorsal tubercle rows (16–17) and high number of tubercles (45–47) in parasagittal row (TubRow), enlarged tubercles on dorsal surface of hindlimb, and no precloacal pores in females (unknown for males).

Note that Zug and Fisher (2012) labeled the subcaudals as keeled but that these are tiny regenerate scales and not typical subcaudal enlarged scales. Genetic relationship to *N. galgajuga* would suggest unregenerated subcaudals are smooth.

Coloration in life is similar to only one other *Nactus*, *N. galgajuga*, in the possession of bold coloration. Dorsally, adult is yellow and dark brown and yellow in 6 irregularly edged transverse bands from the neck to the base of the tail.

ETYMOLOGY. The specific name derives from the local Nali language's term for bumblebee.

DISTRIBUTION. Presently known from the type locality and below the summit of Mount Sabomu (Richards and Aplin, 2015), although potentially widespread in the forested hills of Manus Island (sample 26).

Nactus pelagicus (Girard, 1857)

Pacific Slender-toed Gecko

Gymnodactylus Arnouxii A. Duméril, 1851:44, *nomen oblitum* [type locality: "Nouvelle-Zélande"; holotype, MNHN 5210].

Heteronota pelagica Girard, 1857:197 [type locality: "Feejee and Navigator Islands," restricted to Ovalau, Fiji (Zug and Moon, 1995:88); lectotype, USNM 5626].

DEFINITIONS:

Oceania: A unisexual taxon of geckos (Gekkoninae) with moderate to large adults (♀♀ 48–71 mm SVL) with keeled subcaudals, no or small postmental scales (typically ≤ 6), usually postmental-infralabial (≥ 1) contact, moderate number of dorsal tubercle rows (15–18) and moderate to high number of tubercles (19–35) in parasagittal row (TubRow), enlarged tubercles on dorsal surface of hindlimb, and no precloacal pores (the preceding description is from Zug and Moon, 1995).

Manus: A unisexual taxon of geckos (Gekkoninae) with moderate to large adults (♀♀ 49–61 mm SVL) with keeled subcaudals, moderate postmental scales (8–18), no postmental-infralabial (0) contact, moderate number of dorsal tubercle rows (12–19) and moderately high number of tubercles (28–37) in parasagittal row (TubRow), enlarged tubercles on dorsal surface of hindlimb, and usually no precloacal pores (preceding from Manus Island data, sample 26, and Zug and Fisher, 2012).

Bougainville: A unisexual taxon of geckos (Gekkoninae) with moderate to large adults (♀♀ 52–62 mm SVL) with keeled subcaudals, small to moderate postmental scales (usually ≤ 6), usually postmental-infralabial (≥ 1) contact, moderate number of dorsal tubercle rows (14–19) and moderately high number of tubercles (26–33) in parasagittal row (TubRow), enlarged tubercles on dorsal surface of hindlimb, and no precloacal pores (preceding from Bougainville data, sample 33).

ETYMOLOGY. The choice of *pelagicus* was not stated. It derives from the Greek adjective *pelagikos* for "of the sea."

DISTRIBUTION. *Nactus pelagicus* is widespread throughout the western Pacific from the Northern Mariana Islands southward through Micronesia to Palau and New Guinean islands of Manus and Bougainville (samples 27, 33). In the central Pacific, populations occur from Samoa and Tonga to

southern Vanuatu, with outliers in Polynesia on Nassau Island (Cook Islands), Aki Aki (Tuamotu), and a nineteenth century record from Tahiti.

In Papua New Guinea, populations of a unisexual *Nactus* occur on two islands, Manus and Bougainville (samples 26, 33). I consider these populations to be recently established via the movement of cargo during and immediately after World War II because at present there are no vouchers from PNG prior to 1940. I noted earlier the possibility of the Mussau–St. Mathias population being unisexual; however, the sample is small (two adults) without proof positive of the absences of postmental scales, so I am reluctant to declare them unisexuals, especially when many of their features match the larger sample from nearby Emirau–St. Mathias. The Mussau sample was collected prior to World War II.

Richards and Aplin (2015) performed rapid assessment surveys in Manus and Mussau in 2014 and discovered *N. "pelagicus"* in the two sites surveyed in Mussau and none at the three sites on Manus. The absence on Manus contrasts sharply with the vouchers available in museums. My Manus sample (26) contained 32 females, and during data collection, I ignore museum specimens that were poorly preserved. Their absence in less disturbed areas away from the main human population areas (i.e., those surveyed by Richards and Aplin) suggests that the Manus unisexual has not successfully invaded primary forest and well-developed secondary forests and "village islands" in the forest. The Mussau *N. pelagicus* sample of Richards and Aplin may be unisexual, but they did not examine the gonads or otherwise determine the sex of individuals within their sample.

An extralimital record of *N. cf. pelagicus* from the Talaud Islands (Koch et al., 2009) further suggests the accidental transfer of this unisexual species to islands west of its "natural" distribution in Oceania. I have not examined this specimen (ZMB Lace 5086) but find the description sufficient to accept the Koch et al. identification. I note, however, that their HindfLm count of 19 is just below the range of the Manus, Bougainville, and Oceania unisexual specimens.

COMMENTS. In 1983 when Kluge established the genus *Nactus* and resurrected the name *Gymnodactylus arnouxii* A. Duméril, 1851 as the type species of this new genus, I objected to the reappearance of *arnouxii* as a replacement for the widely used and familiar *pelagica* Girard, 1857. In a small series of articles culminating with my request (Zug, 1989) to the International Commission on Zoological Nomenclature (ICZN) for the suppression of *arnouxii* and Kluge's counter argument (Kluge, 1989) for its retention, the matter was settled by the commission (ICZN, 1991, Opinion 1647). The commission retained the current usage of *pelagicus* and, although not suppressing *arnouxii*, retained it as *nomen oblitum* in case the New Caledonian populations of unisexual *Nactus* were a distinct species. See the discussion in Geographic Patterns section for the likelihood of New Caledonia being an incorrect substitution for the erroneous New Zealand type locality.

***Nactus robertfisheri*, new species**
Bismarcks Slender-toed Gecko

HOLOTYPE. BPBM 22014, adult male from Papua New Guinea, West New Britain Province, Camp 2, 2.6 km NNW of Marmar -5.49° 151.4893° , collected by Fred Kraus on 5 March 2005 (Figure 20).

PARATYPES. BPBM 22012, 22015, 22018, 22021, adult females, and BPBM 22010, 22017, 22024, adult males with the same collecting locality as the holotype on 5–7 March 2005.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with moderate to large adults (♀♀ 50–70 mm, ♂♂ 48–67 mm SVL) with keeled subcaudals, variable-sized postmental scales (2–24, usually ≤ 10), no or slight postmental-infralabial (PmLab = 0–2) contact, low to moderate number of dorsal tubercle rows (14–19) and moderate number of tubercles (24–44, usually ≥ 28) in parasagittal row (TubRow), tubercles on dorsal surface of thigh and crus, and variable precloacal pores (8, 0–12) in males (females usually without pores, 0, 0–1). Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 61.5 mm SVL, tail length not recorded, 25.1 mm TrunkL, 25.3 mm SnForel, 16.9 mm HeadL, 11.8 mm HeadW, 7.5 mm HeadH, 3.9 mm EyeD, 5.4 mm NarEye, 4.3 mm Interorb, 2.5 mm

SnW. Body proportions: 41% TrunkL/SVL, 41% SnForel/SVL, 28% HeadL/SVL, 19% HeadW/SVL, 70% HeadW/HeadL, 6% EyeD/SVL, 23% EyeD/HeadL, 32% NarEye/HeadL, 25% Interorb/HeadL, 15% SnW/HeadL.

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal trapezoidal rostral scale posterior with cleft on midline of middorsal third and lightly depressed on its mid-posterior half; 4 large supralabials and 3 infralabials in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 3 enlarged granular loreal scales, dorsalmost one largest. Supranasals moderate sized, in contact on midline. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large trapezoidal mental and modest postmentals (Postm = 14) touching first supralabial (PmLab = 0). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach to middle of sides, 16 entire rows (DorsTub); tubercles in each row usually separated by more than 1 granular scale, yielding 33 tubercles per row (TubRow); 9 rows transversely between hindlimbs (TubHip). Some enlarged tubercles on dorsal surface of forelimb; hindlimb also with enlarged tubercles (TubHindl = 2) on dorsal surface of thigh and crus. Tail with small uniform scales dorsally and laterally; ventrally with uniform, small smooth scales (Subcaud = 1). Two cloacal spurs (CloacS) on each side, distal edge irregular (CSTip = 1). Ventral scales from chin to vent small, granular, and somewhat larger on chest and abdomen. Precloacal pores 5. Forefoot with narrow digits; 18 lamellae beneath fourth digit (4FingLm), 6 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, 22 lamellae beneath fourth digit (4ToeLm).

Coloration in life not reported. In alcohol, dorsal background medium rufous brown from snout to sacrum; top of head nearly unicolor; series of dark-brown transverse marks from nape onto tail; nape and axillary marks entire, trunk onto sacrum ones divided medially into pairs, all posteriorly narrowly edged in tan or cream. Forelimbs dorsally unicolor as trunk, hindlimbs same color with dark bands, diffuse on thigh and distinct on crus. Venter unicolor rufous brown.

ETYMOLOGY. The specific name recognizes Robert N. Fisher for his biological discoveries in Papua New Guinea and throughout the eastern Pacific. The name also acknowledges our friendship and his ever-ready support of my research endeavors in Pacific herpetology. The specific name is a noun in apposition.

VARIATION. Females and males display slight metric differences (adult ♀♀ 61.1, 50.7–69.5 mm; adult ♂♂ 58.3, 48.2–66.7 mm SVL), although sharing similar proportions (total adult sample): TrunkL/SVL 39.5%, 29%–46%; HeadL/SVL 27.2%, 25%–31%; HeadW/SVL 18.0%, 15%–21%; HeadW/HeadL 66.4%, 56%–76%; EyeD/SVL 6.5%, 5%–8%; EyeD/HeadL 24.1%, 20%–28%; NarEye/HeadL 32.6%, 30%–43%; Interorb/HeadL 26.2%, 21%–31%; SnW/HeadL 14.0%, 11%–18%.

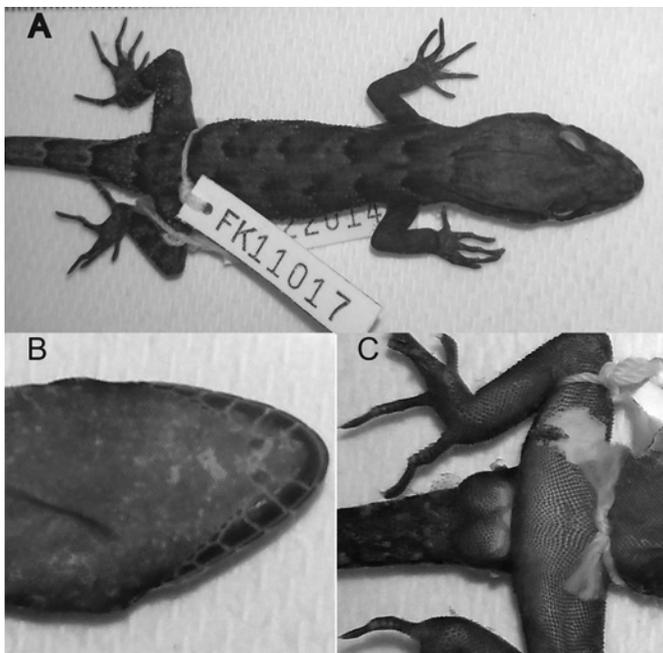


FIGURE 20. Holotype of *Nactus robertfisheri* (BPBM 22014). (A) Dorsal view of entire body, (B) ventral view of head, and (C) ventral view of pelvis and thigh. (Photographs by Molly Hagemann, BPBM.)

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (3, 3–4) and infralabials (3, 2–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and usually moderately large postmentals (Postm = 14, 2–24) and usually no genial scale between postmental and first surpalabial (0, 0–2 PmLab); dorsally, trunk with 16, 14–19 (DorsTub) enlarged tubercles transversely on dorsum and with 30, 24–44 tubercles (TubRow) longitudinally along trunk; 9, 7–10 tubercle rows transversely between hindlimbs (TubHip). Uniform covering of small tuberculate-like scale on dorsal half of forelimb and enlarged tubercles on crus and femur (TubHindl = 2). Tail with small uniform scales dorsally and laterally, ventrally typically with uniform, small keeled scales (Subcaud = 0, 0–1). Usually, single cloacal spurs (1, 1–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 0–12, females 0–1. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 > 5 > 1$; 18, 15–21 lamellae beneath fourth digit (4FingLm), 5, 4–7 scale rows on palm; hindfoot with narrow digits, their lengths $4 \approx 3 > 2 \approx 5 > 1$; 23, 20–25 lamellae beneath fourth toe (4ToeLm).

Coloration in life, individual from West New Britain with medium-brown dorsal and lateral background and broad transverse brown bars on neck (1) to base of tail; 5 on trunk and sacrum, each edged posteriorly with dark brown; broad dark-brown postorbital bar to angle of jaw and dark-brown lips with narrow cream sutures. In alcohol, background tan to medium brown dorsally and ventrally. Top of head with scattered, irregular medium-brown marks (faded mottling), supra- and infralabial scales tan centered, cream edged; small brown postorbital stripe from bottom of orbit to end of temporal area and above ear opening. Dorsally, from base of neck to inguinal area, 5 to 7 brown, irregular-shaped transverse marks, each with cream posterior edge (some divided on midline). Dorsally, base of tail and onward with bold dark bar separated by cream to light-tan interspaces. Venter uniform light tan from chin onto tail.

DISTRIBUTION. Present on the islands of the Bismarck Archipelago (provinces of New Ireland, West New Britain, East New Britain, and Bougainville), Papua New Guinea (samples 27, 28, 30, 31, 32, 33).

***Nactus kamiali*, new species** **Kamiali Slender-toed Gecko**

HOLOTYPE. BPBM 25964, adult female from Papua New Guinea, Morobe Province, Kamiali Wildlife Management Area, 1.3 km N and 6.2 km W of Cape Dinga, -7.296° 147.093° , collected by Allen Allison on 5 September 2004 (Figure 21).

PARATYPES. BPBM 25965, 25967–968, PNGM 17181, adult females, BPBM 25971, adult male with same collecting

data as holotype; USNM 576310, adult male, CAS 249851, adult female, from Kamiali village, Kamiali Biological Research Station, $7^{\circ}17'45.348''S$, $147^{\circ}05'58.524''E$, Morobe Province, Papua New Guinea, collected by R. N. Fisher, J. Stanford, J. Richmond, and B. Iova on 22 May 2010.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with large adults (♀♀ 61–73 mm, ♂♂ 60–70 mm SVL) with keeled subcaudals, variable-sized postmental scales (2–19, usually ≥ 8), no or slight postmental-infralabial (PmLab = 0–1) contact, moderate number of dorsal tubercle rows (17–20) and moderate number of tubercles (27–34, usually ≥ 28) in parasagittal row (TubRow), tubercles on dorsal surface of thigh and crus, and precloacal pores (9, 8–11) in males, females lack pores (0). Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 71.9 mm SVL, tail length not recorded, 28.9 mm TrunkL, 29.7 mm SnForel, 20.1 mm HeadL, 14.3 mm HeadW, 9.3 mm HeadH, 4.7 mm EyeD, 6.4 mm NarEye, 4.8 mm Interorb, 2.7 mm SnW. Body proportions: 40% TrunkL/SVL, 41% SnForel/SVL, 28% HeadL/SVL, 20% HeadW/SVL, 71% HeadW/HeadL, 6% EyeD/SVL, 23% EyeD/HeadL, 32% NarEye/HeadL, 24% Interorb/HeadL, 13% 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 two-thirds and slightly depressed on its mid-posterior half; 3 large supralabials (right) and 3 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of

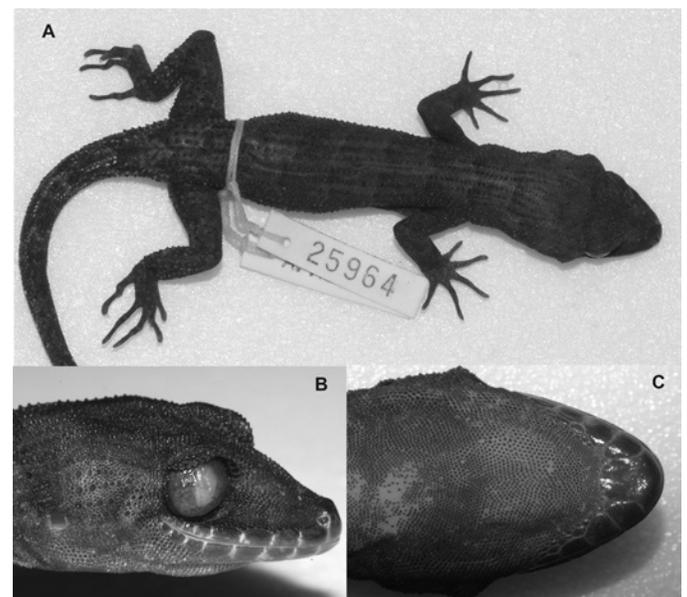


FIGURE 21. Holotype of *Nactus kamiali* (BPBM 25964). (A) Dorsal view of entire body, (B) lateral view of head, and (C) ventral view of head. (Photographs by M. Hagemann, BPBM.)

respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 3 granular loreal scales, upper largest. Supranasals moderate sized, rounded posteriorly, anteriorly touching on midline, posteriorly, granular scales fill midline space created by rounded corners. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large, nearly longitudinally rectangular mental and very small postmentals (Postm = 2). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach ventrolaterally to edge of venter, 19 entire rows (DorsTub), and to mid-laterally on neck; tubercles in each row usually separated by 2 granular scales, yielding 34 tubercles per row (TubRow); 10 rows transversely between hindlimbs (TubHip). No tubercles on dorsal half of upper arm, widely scattered small tubercles on forearm; hindlimb with tubercles on upper and lower limbs (TubHindl = 2), and tubercles moderately abundant fore and aft (TubDens = 2). Tail anteriorly with tubercle rows dorsally, laterally, and slightly overlapping onto ventral surface. Tail ventrally with uniform small keeled scales (Subcaud = 0). Pair of cloacal spurs (CloacS) on right and left; distal edge rounded (CSTip = 0). Ventral scales from chin to vent small, granular, and unicaninate. No precloacal pores. Forefoot with narrow digits, their lengths $3 \approx 4 > 2 > 5 \approx 1$; 18 lamellae beneath fourth digit (4FingLm), 6 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 22 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as row of greatly enlarged scales.

Coloration in life not reported. In alcohol, background brown dorsally and laterally, venter lighter brown. Top of head darker dusky brown from interorbital to tip of snout; diffuse dusky-brown transverse bars begin on neck (2) and continue to base of tail (5 on trunk), small, irregular blotch on sacrum and base of tail. Limbs patternless brown above and hindlimbs without contrasting striping on thighs, although some small, whitish spots below ventral surface of limbs as trunk.

ETYMOLOGY. The specific name derives directly from the geographic place name, Kamiali, where the first specimens were discovered by Allen Allison.

VARIATION. Females and males display slight metric differences (adult ♀♀ 67.3, 61.5–73.1 mm; adult ♂♂ 66.8, 59.5–69.5 mm SVL), although sharing similar proportions (total adult sample): TrunkL/SVL 38.6%, 35%–45%; HeadL/SVL 27.8%, 27%–29%; HeadW/SVL 18.2%, 15%–20%; HeadW/HeadL 65.6%, 56%–71%; EyeD/SVL 6.7%, 6%–8%; EyeD/HeadL 24.1%, 21%–29%; NarEye/HeadL 33.2%, 30%–43%; Interorb/HeadL 25.2%, 22%–30%; SnW/HeadL 14.5%, 13%–16%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (4, 3–4) and infralabials (3.5, 3–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and usually moderate-sized postmentals (Postm = 10,

2–19) and usually no genial scale between postmental and first supralabial (0, 0–1 PmLab); dorsally, trunk with 19, 17–20 (DorsTub) enlarged tubercles transversely on dorsum and with 30, 27–34 tubercles (TubRow) longitudinally along trunk; 10, 8–10 tubercle rows transversely between hindlimbs (TubHip). Uniform covering of small tuberculate-like scale on dorsal half of forelimb and enlarged tubercles on crus and femur (TubHindl = 2). Tail with small uniform scales dorsally and laterally, ventrally typically with uniform, small keeled scales (Subcaud = 0, 0–1). Usually, single cloacal spurs (1, 1–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 8–11, females 0. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 > 5 > 1$; 18, 16–19 lamellae beneath fourth digit (4FingLm), 5, 4–7 scale rows on palm; hindfoot with narrow digits, their lengths $4 \approx 3 > 2 \approx 5 > 1$; 22, 20–23 lamellae beneath fourth toe (4ToeLm).

Coloration in life, dorsal and lateral background variable light to medium brown with distinct to diffuse dark transverse bars middorsally continuous or separated, usually dark nape bar and always mid-cervical bar, 5 bars from shoulder to trunk; dark-brown sacral and first caudal bars always evident; top of head unicolor to scattered dark marks. Dorsally, limbs usually dark brown mottled, posterior thighs of most individuals with pair of dark horizontal stripes enclosing near-white stripe. In alcohol, background tan to medium brown dorsally and laterally. Top of head with medial darker-brown figure from interorbital onto snout, supralabials large, brown with white to cream posterior margin, infralabials cream to dusky white. Nearly uniform tan dorsally from crown onto base of tail. Venter uniform light tan from chin onto tail.

DISTRIBUTION. Along the coast and adjacent mountains from central Morobe Province (Kamiali) to Northern Province (Mount Lamington; samples 34, 35, 36; Figure 22).

Collingwood Bay population (unassigned)

COMMENTS. There are only three decently preserved specimens from the localities in the vicinity of Collingwood Bay: an adult male and two adult females. They do not closely match the *kamiali* or D'Entrecasteaux paradigm, hence my reluctance to assign them to those taxa and equal reluctance to recognize them as representatives of a unique population.

DESCRIPTION. Females and male are similar in size (adult ♀♀ 48.8, 44.5–53.01 mm; adult ♂ 45.9 mm SVL) and share similar proportions (total adult sample): TrunkL/SVL 40.1%, 39%–41%; HeadL/SVL 28.5%, 28%–29%; HeadW/SVL 18.9%, 19%–19%; HeadW/HeadL 66.2%, 65%–71%; EyeD/SVL 8.1%, 8%–9%; EyeD/HeadL 27.9%, 27%–31%; NarEye/HeadL 32.5%, 32%–33%; Interorb/HeadL 31.0%, 30%–34%; SnW/HeadL 16.7%, 13%–17%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Large supralabials (4) and infralabials (4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and moderate-sized postmentals (Postm = 14,

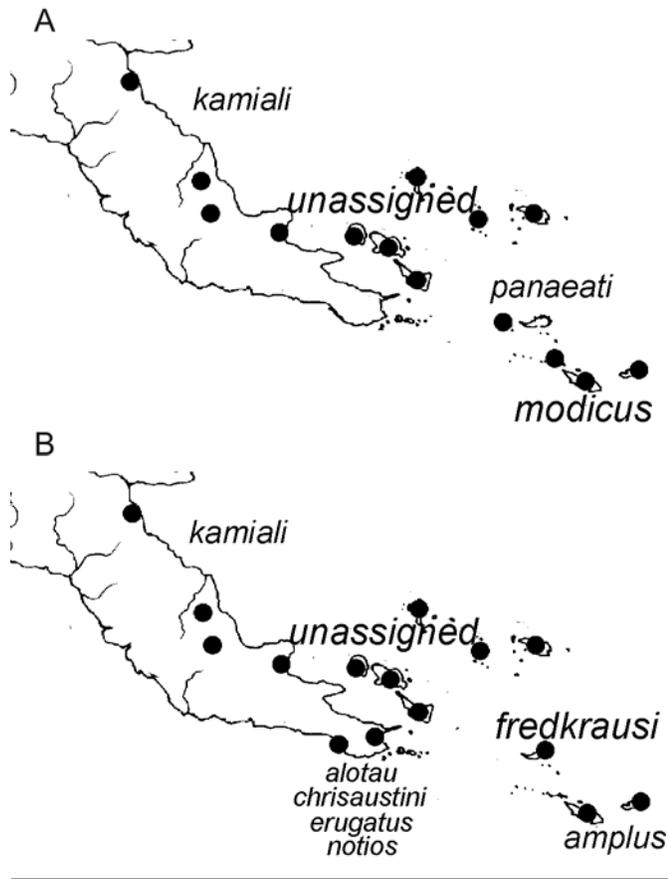


FIGURE 22. Occurrence of *Nactus* species on the north coast of peninsular Papua New Guinea, mainland Milne Bay, D'Entrecasteaux Islands, Trobriand Islands, and Louisiade Archipelago. The solid circles are sample localities identified in Figure 1. (A) *Nactus kamiali* on the mainland and *N. panaeati*, *N. modicus*, and unassigned *Nactus* populations in the islands. (B) *Nactus alotau*, *chrisaustini*, *erugatus*, and *notios* on the mainland and *N. fredkrausi* and *N. amplus* in the islands.

8–18) and no genial scale between postmental and first supralabial (0); dorsally, trunk with 16–17 (DorsTub) enlarged tubercles transversely on dorsum and with 28, 25–32 tubercles (TubRow) longitudinally along trunk; 10 tubercle rows transversely between hindlimbs (TubHip). Enlarged tubercles on crus and femur (TubHindl = 2). Tail with small uniform scales dorsally and laterally, ventrally typically with uniform, small keeled scales (Subcaud = 0). Two cloacal spurs on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, male 10, females 0. Forefoot with narrow digits, 18–19 lamellae beneath fourth digit (4FingLm), 5–6 scale rows on palm; hindfoot with narrow digits, 22, 22–24 lamellae beneath fourth toe (4ToeLm).

Coloration in life from photograph (Tan, 2016), background tan to medium brown dorsally and laterally. Top of head

with brown X-shaped mark on snout, dusky-brown interorbital area, and crown medium brown; indistinct dark-brown postorbital stripe to above tympanum. Dorsally, neck and trunk to base of tail with series of paired dark-brown, cream-edged posterior spots on dorsum becoming chevron-like on rear of trunk and base of tail; laterally, trunk with ill-defined brown bars.

DISTRIBUTION. Localities represented are Binigui, Menapi, Kwagiri River, and Mount Dayman (sample 37).

North Milne Bay Island populations (unassigned)

COMMENTS. Initially, I considered that the various island populations represented several different species. Their slight differentiation from one another and their similarity to the common mainland Milne Bay *Nactus* populations, which I am recognizing as a distinct and widespread species on the south coast of Papua New Guinea, suggest that these insular populations should not be named either as new species or, for the moment, assigned to another species.

DESCRIPTION. The *Nactus* populations on the islands north of the Milne Bay mainland show some differentiation among the islands, but it is insufficient to segregate them nomenclaturally. The populations, individually and as a group, share features of the most abundant Milne Bay morphotype (*alotau*), although I am presently reluctant to formally associate them with that morphotype. Within the islands, I recognize three morphotypes: D'Entrecasteaux, Normanby, and Trobriand.

The D'Entrecasteaux morphotype derives from the Good-enough and Fergusson Islands (samples 38, 39).

These bisexual geckos have moderate to large adults; females and males display slight metric differences (adult ♀♀ 61.6, 45.1–74.3 mm; adult ♂♂ 65.0, 50.1–68.5 mm SVL), although sharing similar proportions (total adult sample): TrunkL/SVL 40.8%, 37%–47%; HeadL/SVL 27.9%, 26%–39%; HeadW/SVL 17.7%, 16%–19%; HeadW/HeadL 63.7%, 47%–68%; EyeD/SVL 5.9%, 6%–9%; EyeD/HeadL 25.1%, 19%–32%; NarEye/HeadL 31.9%, 19%–35%; Interorb/HeadL 26.7%, 21%–32%; SnW/HeadL 14.3%, 10%–17%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (4, 3–4) and infralabials (3, 3–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and usually moderate-sized postmentals (Postm = 14, 6–24) and usually no genial scale between postmental and first supralabial (0, 0–1 PmLab); dorsally, trunk with 16, 13–16 (DorsTub) enlarged tubercles transversely on dorsum and with 30, 25–40 tubercles (TubRow) longitudinally along trunk; 8, 8–11 tubercle rows transversely between hindlimbs (TubHip). Uniform covering of small tuberculate-like scale on dorsal half of forelimb and enlarged tubercles on crus and femur (TubHindl = 2). Tail with small uniform scales dorsally and laterally, ventrally typically with uniform, small keeled

scales (Subcaud = 0, 0–1). Usually, single cloacal spurs (2, 0–3 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 2–13, females 0. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 > 5 > 1$; 18, 13–21 lamellae beneath fourth digit (4FingLm), 6, 2–8 scale rows on palm; hindfoot with narrow digits, their lengths $4 \approx 3 > 2 \approx 5 > 1$; 20, 19–27 lamellae beneath fourth toe (4ToeLm).

The Normanby morphotype derives from Normanby Island (sample 40) of the D'Entrecasteaux Islands. It consists of moderate to large bisexual geckos. Females and males display slight metric differences (adult ♀♀ 54.2, 47.2–64.3 mm; adult ♂♂ 50.8, 45.0–55.4 mm SVL), although sharing similar proportions (total adult sample): TrunkL/SVL 40.7%, 37%–48%; HeadL/SVL 26.8%, 25%–28; HeadW/SVL 17.8%, 17%–19%; HeadW/HeadL 66.8%, 56%–71%; EyeD/SVL 6.2%, 6%–9%; EyeD/HeadL 25.1%, 23%–32%; NarEye/HeadL 32.8%, 31%–34%; Interorb/HeadL 29.9%, 25%–34%; SnW/HeadL 15.3%, 13%–18%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (3, 2–4) and infralabials (3, 2–3) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and small to moderate postmentals (Postm = 8, 2–16) and usually no genial scale between postmental and first supralabial (0, 0–1 PmLab); dorsally, trunk with 18, 15–20 (DorsTub) enlarged tubercles transversely on dorsum and with 27, 24–34 tubercles (TubRow) longitudinally along trunk; 8, 8–10 tubercle rows transversely between hindlimbs (TubHip). Enlarged tubercles on crus and femur (TubHindl = 2). Tail with small uniform scales dorsally and laterally, ventrally typically with uniform, small keeled scales (Subcaud = 0). Usually, pair of cloacal spurs (2, 1–2 CloacS) on each side. Precloacal pores, males 0–8, females 0. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 > 5 > 1$; 16, 16–18 lamellae beneath fourth digit (4FingLm), 5, 4–7 scale rows on palm; hindfoot with narrow digits, their lengths $4 \approx 3 > 2 \approx 5 > 1$; 21, 19–22 lamellae beneath fourth toe (4ToeLm).

The Trobriand morphotype derives from three sets of islands: Kiriwina and Kuia (#41), Yanaba in the Egum Atoll (#42), and Woodlark Island (#43). These bisexual geckos (Gekkoninae) have moderate-sized adults. Females and males display slight metric differences (adult ♀♀ 52.1, 43.1–56.9 mm; adult ♂♂ 49.6, 45.8–53.8 mm SVL), although sharing similar proportions (total adult sample): TrunkL/SVL 39.2%, 36%–44%; HeadL/SVL 27.8%, 26%–29%; HeadW/SVL 18.0%, 16%–20%; HeadW/HeadL 64.9%, 55%–70%; EyeD/SVL 7.3%, 7%–8%; EyeD/HeadL 26.2%, 24%–30%; NarEye/HeadL 31.3%, 26%–36%; Interorb/HeadL 28.8%, 23%–33%; SnW/HeadL 14.5%, 12%–17%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (4, 3–5) and infralabials (3, 3–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and small to moderate postmentals (Postm = 10, 2–18) and usually no genial scale between postmental and first supralabial (0, 0–1 PmLab); dorsally, trunk with 15, 12–18 (DorsTub) enlarged tubercles transversely on dorsum and with 29, 24–33 tubercles (TubRow) longitudinally along trunk; 9, 7–10 tubercle rows transversely between hindlimbs (TubHip). Enlarged tubercles on crus and femur (TubHindl = 2), rarely on only crus. Tail with small uniform scales dorsally and laterally, typically with uniform, small keeled scales ventrally (Subcaud = 0). Usually, pair of cloacal spurs (2, 1–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 1–9, females 0. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 \approx 5 > 1$; 18, 14–20 lamellae beneath fourth digit (4FingLm), 5, 4–6 scale rows on palm; hindfoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 22, 20–24 lamellae beneath fourth toe (4ToeLm).

Nactus fredkrausi, new species

Kraus's Giant Slender-toed Gecko

HOLOTYPE. BPBM 16749, adult male from Papua New Guinea, Milne Bay Province, Misima Island, Oya Tau, "Camp 2," 860 m asl, 10°39.355'S 152°37.659'E, collected by Fred Kraus on 18 January 2003 (Figure 23).

PARATYPES. BPBM 16742, 16746, 16751, 16753, adult females, and BPBM 16745, 16750, 16752, adult males; all from Misima Island and collected by Fred Kraus. BPBM 16742, 16745–746 from Bwaga Bwaga ridge camp, -10°42.437' 152°40.971', 350–400 m, collected on 12 January 2003; BPBM 16750–753 with the same collecting data as the holotype.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with large adults (♀♀ 57–77 mm, ♂♂ 52–74 mm SVL) with keeled subcaudals, variable-sized postmental scales (8–22, median 14), no or slight postmental-infralabial contact (PmLab = 0–1, median 0), moderate number of dorsal tubercle rows (16–19) and moderate number of tubercles (26–33, usually ≥ 29) in parasagittal row (TubRow), tubercles present on dorsal surface of thigh and crus, and precloacal pores present in males (4–7), usually present in females (0–7). Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 74.2 mm SVL, 29.9 mm TrunkL, 30.7 mm SnForel, 20.8 mm HeadL, 16.3 mm HeadW, 8.0 mm HeadH, 5.1 mm EyeD, 5.1 mm NarEye, 5.0 mm Interorb, 3.0 mm SnW. Body proportions: 40% TrunkL/SVL, 41% SnForel, 28% HeadL/SVL, 15% HeadW/SVL, 54% HeadW/HeadL, 7% EyeD/SVL, 25% EyeD/HeadL, 34% NarEye/HeadL, 24% Interorb/HeadL, 14% SnW/HeadL.

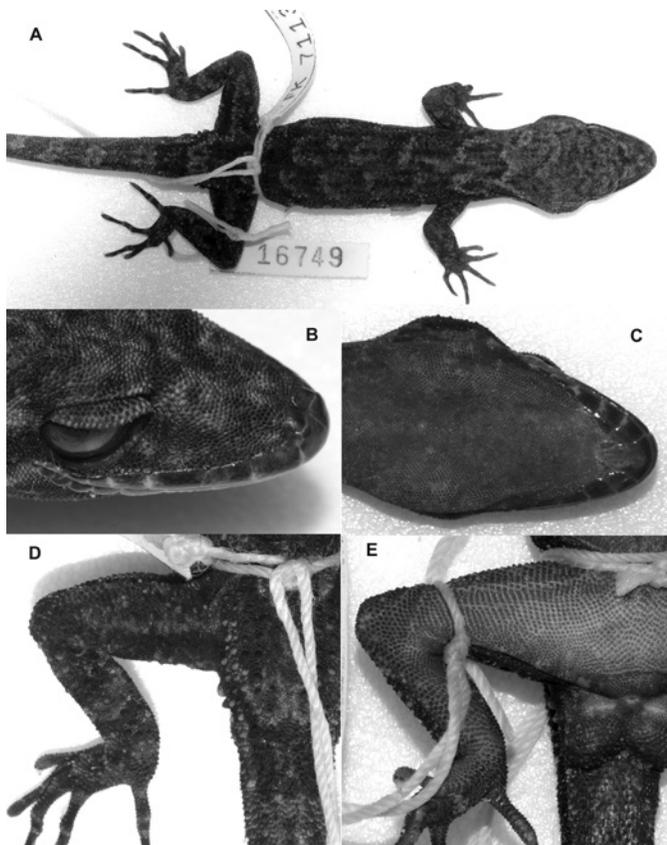


FIGURE 23. Holotype of *Nactus fredkrausi* (BPBM 16749). (A) Dorsal view of entire body, (B) dorsolateral view of snout, (C) ventral view of head, (D) dorsal of pelvis and thigh, and (E) ventral view of pelvis and thigh. (Photographs by M. Hagemann, BPBM.)

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal, round-edged rectangular rostral scale with distinct posteromedial depression bearing midline cleft of posterior half; 3 large supralabials (left and right, Suplab) and 4 infralabials (left and right, Inflab) in front of anterior edge of orbit, first supra- and second infralabials largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal and posteriorly 2 postnasal scales, dorsal one 3 times the size of ventral one. Supranasals moderate sized, separated on midline by large internasal. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large triangular mental and pair of large postmentals (Postm = 18). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; and mid-laterally on trunk, 16 entire rows (DorsTub), and only to mid-laterally on neck; tubercles in each row usually separated by single granular scale yielding 32 tubercles per row (TubRow); 10 rows transversely between hindlimbs (TubHip). Enlarged tubercles on

dorsal half of forelimb; hindlimb with tubercles abundant fore and aft on thigh and crus (TubHindl = 2; TubDens = 1). Tail with tubercle rows dorsally, laterally, and slightly overlapping onto ventral surface. Tail entire, uniformly covered dorsally with smooth round scales and ventrally scales similar, slightly larger and smooth (Subcaud = 1). Pair of cloacal spurs (CloacS) on each side, medial one largest; tip smooth edged (CSTip = 1). Ventral scales from chin to vent small, granular to tuberculate. Preloacal pores 5. Forefoot with narrow digits, their lengths $2 \approx 3 > 4 > 1 \approx 5$; 21 lamellae beneath fourth digit (4FingLm), 6 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $3 \approx 4 > 5 > 2 > 1$; 26 lamellae beneath fourth digit (4ToeLm).

In life, coloration not reported. In alcohol, light- to medium-brown background with 4 to 5 dark transverse bars on trunk between axilla and inguinal and a more rectangular-shaped dark bar on neck; the interspaces between dark bars are two-tone light brown anteriorly; rear of thigh distinctly darker brown than dorsally.

ETYMOLOGY. This species is named to recognize Fred Kraus's past and continuing contributions to the systematics and biology of the New Guinea herpetofauna. I also wish to acknowledge our friendship and his ongoing tolerance for answering my questions on New Guinea and the exotic herpetofauna of Hawaii. The specific name is a noun in apposition.

VARIATION. Females and males display slight metric differences (adult ♀♀ 67.6, 57.1–76.5 mm; adult ♂♂ 66.1, 52.0–74.2 mm SVL) and share similar proportions (total adult sample): TrunkL/SVL 39.0%, 33%–42%; HeadL/SVL 28.7%, 28%–30%; HeadW/SVL 17.0%, 15%–18%; HeadW/HeadL 59.3%, 53%–66%; EyeD/SVL 7.1%, 7%–8%; EyeD/HeadL 24.8%, 23%–28%; NarEye/HeadL 33.9%, 32%–34%; Interorb/HeadL 25.0%, 22%–28%; SnW/HeadL 13.8%, 13%–15%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (3, 3–4) and infralabials (3, 3–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and usually moderate-sized postmentals (Postm = 14, 8–22) and usually no genial scale between postmental and first supralabial (0, 0–1 PmLab); dorsally, trunk with 18, 16–19 (DorsTub) enlarged tubercles transversely on dorsum and with 29, 26–33 tubercles (TubRow) longitudinally along trunk; 10, 8–11 tubercle rows transversely between hindlimbs (TubHip). Uniform covering of small tuberculate-like scale on dorsal half of forelimb and enlarged tubercles on femur (TubHindl = 1). Tail with small uniform scales dorsally and laterally, ventrally typically with uniform, small keeled scales (Subcaud = 0). Usually, paired cloacal spurs (2, 0–4 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Preloacal pores, males 4–7, females 0–6, most with pores. Forefoot with narrow digits, their lengths usually

3≈4>2>5>1; 19, 17–21 lamellae beneath fourth digit (4FingLm), 6, 5–7 scale rows on palm; hindfoot with narrow digits, their lengths 4≈3>2≈5>1; 24, 21–26 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, pattern and coloration largely match holotype.

DISTRIBUTION. Known only from the montane forest of central Misima Island, assumed to occur in all forests of Misima (sample 45; Figure 22).

Nactus panaeati, new species

Panaeati Slender-toed Gecko

HOLOTYPE. AMS R4777, adult male from Papua New Guinea, Milne Bay Province, Panaeati Island [−10.6851° 152.3727°], collected by A. H. S. Lucas on 04 April 1910 (Figure 24).

PARATYPES. AMS R4779, adult female, and AMS R4778, adult male; both with same collecting data as holotype.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with moderate adults (♀ 48 mm, ♂♂ 44–50 mm SVL) with keeled subcaudals, medium-sized postmental scales (14–16), no or slight postmental-infralabial contact (PmLab = 0–1), low number of dorsal tubercle rows (15–17) and moderate number of tubercles (25–27) in parasagittal row (TubRow), tubercles on dorsal surface of thigh and crus, and precloacal pores, males 7–8, females 0. Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 49.8 mm SVL, tail length not recorded, 18.8 mm TrunkL, 19.3 mm SnForel, 13.8 mm HeadL, 8.8 mm HeadW, 6.6 mm HeadH, 3.5 mm EyeD, 4.5 mm NarEye, 4.2 mm Interorb, 2.3 mm SnW. Body proportions: 38% TrunkL/SVL, 39% SnForel/SVL, 28% HeadL/SVL, 18% HeadW/SVL, 64% HeadW/HeadL, 7%



FIGURE 24. Holotype of *Nactus panaeati* (AMS R4777). Dorsal view of entire body. (Photograph by S. Mahony, AMS.)

EyeD/SVL, 25% EyeD/HeadL, 33% NarEye/HeadL, 30% Interorb/HeadL, 17% 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 two-thirds and slightly depressed on its mid-posterior half; 3 large supralabials (right) and 3 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 3 granular loreal scales, upper largest. Supranasals moderate sized, rounded posteriorly, anteriorly touching on midline, posteriorly granular scales fill midline space created by rounded corners. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large, nearly longitudinally rectangular mental and moderate postmentals (Postm = 14). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach ventrolaterally to edge of venter, 15 entire rows (DorsTub), and to mid-laterally on neck; tubercles in each row usually separated by 2 or more granular scales, yielding 26 tubercles per row (TubRow); 9 rows transversely between hindlimbs (TubHip). Hindlimb with tubercles on upper and lower limbs (TubHindl = 2), and tubercles moderately abundant fore and aft (TubDens = 1). Tail anteriorly with tubercle rows dorsally, laterally, and slightly overlapping onto ventral surface. Tail ventrally with uniform small keeled scales (Subcaud = 0). Single cloacal spur (CloacS) on right and left; distal edge rounded (CSTip = 0). Ventral scales from chin to vent small, granular to tuberculate. Precloacal pores, males 7–8, females 0. Forefoot with narrow digits, their lengths 3≈4>2>5≈1; 17 lamellae beneath fourth digit (4FingLm), 6 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths 3≈4>2≈5>1; 21 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as row of greatly enlarged scales.

Coloration in life not recorded. In alcohol, background faded creamy tan dorsally and ventrally. Top of head with few scattered small brownish marks; pair of small faded dark-brown marks on neck, 5 small ones on trunk. Limbs with dark marks on dorsal surface, not arranged in bands.

ETYMOLOGY. The specific name derives directly from the geographic place name of the island of origin.

VARIATION. Females and males share metrics (adult ♀ 48.6 mm; adult ♂♂ 47.0, 44.2–49.0 mm SVL) and share similar proportions (total adult sample): TrunkL/SVL 38.3%, 38%–42%; HeadL/SVL 27.1%, 27%–28%; HeadW/SVL 17.8%, 17%–18%; HeadW/HeadL 65.6%, 64%–69%; EyeD/SVL 7.1%, 7%–8%; EyeD/HeadL 26.1%, 25%–27%; NarEye/HeadL 32.6%, 32%–34%; Interorb/HeadL 30.5%, 30%–31%; SnW/HeadL 16.0%, 15%–17%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small

granular scale (internasal); 3 large supralabials and 3 infralabials in front of anterior edge of eye, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and usually moderate-sized postmentals ($\text{Postm} = 14, 14\text{--}16$) and usually no genial scale between postmental and first supralabial (0, 0–1 PmLab); dorsally, trunk with 15, 15–17 (DorsTub) enlarged tubercles transversely on dorsum and with 26, 25–26 tubercles (TubRow) longitudinally along trunk; 10, 9–10 tubercle rows transversely between hindlimbs (TubHip). Uniform covering of small tuberculate-like scale on dorsal surface of forelimb and enlarged tubercles on crus and femur ($\text{TubHindl} = 2$). Tail with small uniform scales dorsally and laterally, ventrally typically with uniform, small keeled scales ($\text{Subcaud} = 0$). Usually, 2 cloacal spurs (2, 1–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 7–8, females 0. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 > 5 > 1$; 17, 15–17 lamellae beneath fourth digit (4 FingLm), 6, 4–6 scale rows on palm; hindfoot with narrow digits, their lengths $4 \approx 3 > 2 \approx 5 > 1$; 21, 20–22 lamellae beneath fourth toe (4 ToeLm).

Coloration in life not reported; in alcohol similar to holotype.

DISTRIBUTION. Known only from the island of Pan-aeati (sample 44; Figure 22).

***Nactus modicus*, new species** **Louisiade Slender-toed Gecko**

HOLOTYPE. BPBM 19852, adult male from Papua New Guinea, Milne Bay Province, Sudest Island, track up Mount Rossel, Point 30, small stream below Camp 2, $-11.3543^{\circ} 154.22315^{\circ}$ [Aus66], 640 m. Camp 1, $-11.4918^{\circ} 153.4126^{\circ}$, 127 m asl, along Gesirava River, collected by Fred Kraus, F. Malesa, and local collectors on 9 April 2004 (Figure 25).

PARATYPES. BPBM 19831–832, 19837–838, adult females from Sudest Island, Araeda, $-11.4362^{\circ} 153.4301^{\circ}$, 0 m asl, collected by Fred Kraus on 10 April 2004, and BPBM 19834, locality as preceding male paratypes, and 19853–854, adult males with the same collecting data as the holotype.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with moderate to large adults (♀♀ 46–65 mm, ♂♂ 48–68 mm SVL) with keeled subcaudals, usually large postmental scales (10–28, median 24), no postmental-infralabial ($\text{PmLab} = 0$) contact, moderate number of dorsal tubercle rows (15–21) and moderate number of tubercles (25–32, usually ≥ 28) in parasagittal row (TubRow), tubercles present on dorsal surface of thigh and crus, and precloacal pores (11, 10–14) in males, most females lack pores (0, 0–12). Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 56.4 mm SVL, 21.2 mm TrunkL, 23.2 mm SnForel, 16.7 mm HeadL, 10.5 mm HeadW, 6.7 mm HeadH, 3.7 mm EyeD, 5.2 mm NarEye, 4.3 mm Interorb, 2.2 mm SnW. Body proportions: 38% TrunkL/SVL, 41% SnForel/SVL, 30% HeadL/SVL,

19% HeadW/SVL, 63% HeadW/HeadL, 7% EyeD/SVL, 22% EyeD/HeadL, 31% NarEye/HeadL, 26% Interorb/HeadL, 13% 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 two-thirds and slightly depressed on its mid-posterior half; 3 large supralabials (right) and 3 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 2 granular loreal scales (right, 3 left), upper largest. Supranasals moderate sized, rounded posteriorly, anteriorly touching on midline, posteriorly granular scales fill midline space created by rounded corners. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large, pentagonal mental and very large postmentals ($\text{Postm} = 28$) and no genial scale between postmental and first supralabial. Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach ventrolaterally to near edge of venter, 18 entire rows (DorsTub), and to mid-laterally on neck;

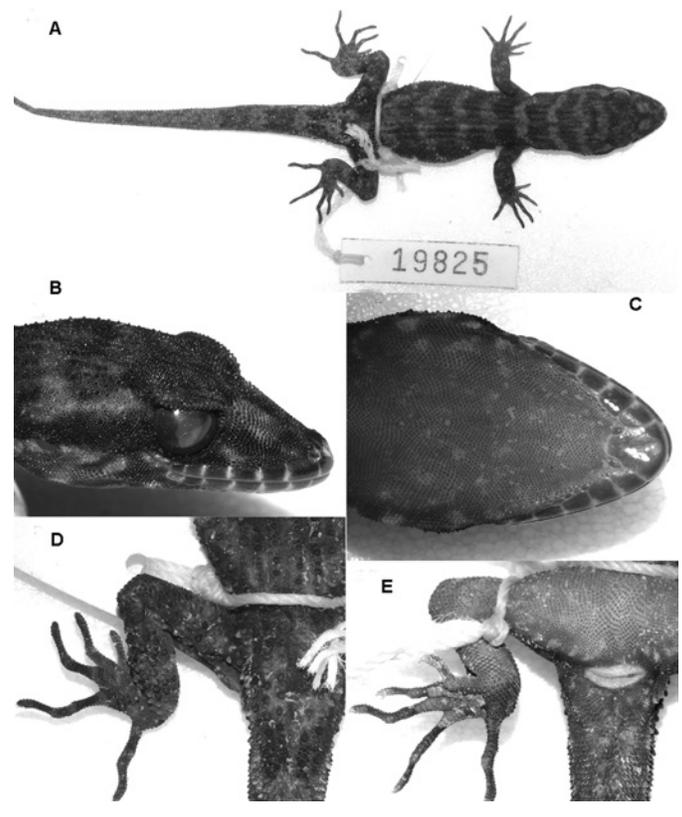


FIGURE 25. Holotype of *Nactus modicus* (BPBM 19852). (A) Dorsal view of entire body, (B) dorsolateral view of snout, (C) ventral view of head, (D) dorsal view of pelvis and thigh, and (E) ventral view of pelvis and thigh. (Photographs by M. Hagemann, BPBM.)

29 tubercles per row (TubRow); 10 rows transversely between hindlimbs (TubHip). Hindlimb with tubercles on upper and lower limbs (TubHindl = 2), and tubercles moderately abundant fore and aft (TubDens = 1). Tail anteriorly with tubercle rows dorsally, laterally, and slightly overlapping onto ventral surface. Tail ventrally with uniform small keeled scales (Subcaud = 0). Precloacal pores 11. Pair of cloacal spurs (CloacS) on right and left; distal edge bluntly rounded (CSTip = 0). Ventral scales from chin to vent small, granular to tuberculate. Forefoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 17 lamellae beneath fourth digit (4FingLm), 4 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 21 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as row of greatly enlarged scales.

Coloration in life not reported. In alcohol, background medium brown dorsally and laterally. Venter medium brown with numerous tan flecks. Dorsally, head with dark-brown figures, dark-rimmed ocelli on snout, interorbital dark smudge. Postorbital and occiput with narrow, flattened W-shaped bars; broad transverse dark-brown nape and cervical bars; 5 broad bars between axilla and inguina; fragmented bar on sacrum and pairs of dark caudal spots, separated or fused medially; fore- and hindlimbs with irregular bands. Head laterally with dark-brown preorbital and postorbital stripes, posterior one broader than anterior one; labial scales dark brown with distinct cream sutures.

ETYMOLOGY. The Latin adjective *modicus* refers to “moderate,” “medium,” or “average” and is proposed for these populations that represent the size range of many New Guinea populations.

VARIATION. Females and males display slight metric differences (adult ♀♀ 58.7, 46.0–64.5 mm; adult ♂♂ 56.5, 47.8–67.9 mm SVL), although sharing similar proportions (total adult sample): TrunkL/SVL 40.2%, 37%–45%; HeadL/SVL 27.7%, 24%–30%; HeadW/SVL 18.5%, 18%–20%; HeadW/HeadL 67.2%, 61%–79%; EyeD/SVL 6.8%, 6%–7%; EyeD/HeadL 24.6%, 21%–28%; NarEye/HeadL 32.4%, 31%–36%; Interorb/HeadL 26.7%, 24%–32%; SnW/HeadL 14.3%, 13%–17%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (3, 3–4) and infralabials (3, 3–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and large postmentals (Postm = 24, 10–28) and no genial scale between postmental and first supralabial (0 PmLab); dorsally, trunk with 18, 15–21 (DorsTub) enlarged tubercles transversely on dorsum and with 28, 25–32 tubercles (TubRow) longitudinally along trunk; 10, 7–12 tubercle rows transversely between hindlimbs (TubHip). Enlarged tubercles on crus and femur (TubHindl = 2). Tail with small uniform scales dorsally and laterally, ventrally variable with uniform, small keeled or

smooth scales (Subcaud = 0, 0–1). Usually, pair of cloacal spurs (2, 0–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 10–14, females 0–12. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 \approx 5 > 1$; 17, 15–19 lamellae beneath fourth digit (4FingLm), 5, 4–6 scale rows on palm; hindfoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 20, 15–23 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, color and pattern match the general description of the holotype.

DISTRIBUTION. On two island banks in the extreme eastern Louisiade Archipelago of Milne Bay Province, Papua New Guinea: Nimo (Nimowa) and Sudest Islands and Rossel (Yela) Island (samples 46, 47, 48; Figure 22).

Nactus amplus, new species

Louisiane Giant Slender-toed Gecko

HOLOTYPE. BPBM 19864, adult female from Papua New Guinea, Milne Bay Province, Rossel Island, track up Mount Rossel, Point 30, small stream below Camp 2, -11.3544° 154.2232° E, collected by Fred Kraus, F. Malesa, and local collectors on 9 May 2004 (Figure 26).

PARATYPES. Adult females from Rossel Island, Louisiade Archipelago, Milne Bay Province, Papua New Guinea, AMNH 76752, Mount Rossel, south slope, 700 m, collected by R. F. Peterson on 12–20 October 1956; BPBM 19867, Rossel Island, Camp 3 along Rupu River, -11.3354° 154.2247° , collected by Fred Kraus, F. Malesa, and local collectors on 12 May 2004, and immature female, BPBM 19869, Wupu River crossing, -11.3380° 154.2238° , 278 m, collected by Fred Kraus, F. Malesa, and local collectors on 12 May 2004. Adult females, BPBM 19847, 19848 from Sudest Island, Camp 1, -11.4918° 153.4162° , 127 m elevation, along Gesirava River, collected by Fred Kraus on 16 April 2004.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with large adults (♀♀ 75–82 mm, ♂ 68 mm SVL) with smooth subcaudals, variable-sized postmental scales (6–24, median 12), variable postmental-infralabial (PmLab = 0–2, median 0) contact, moderate number of dorsal tubercle rows (14–20) and moderate number of tubercles (27–32, usually ≥ 29) in parasagittal row (TubRow), tubercles usually present on dorsal surface of thigh and crus, and precloacal pores variable (median 0, 0–14 in females; 14 in male). Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult female, 79.6 mm SVL, 31.6 mm TrunkL, 32.9 mm SnForel, 22.7 mm HeadL, 15.6 mm HeadW, 10.2 mm HeadH, 5.3 mm EyeD, 7.7 mm NarEye, 5.7 mm Interorb, 3.0 mm SnW. Body proportions: 40% TrunkL/SVL, 41% SnForel/SVL, 29% HeadL/SVL, 20% HeadW/SVL, 69% HeadW/HeadL, 7% EyeD/SVL, 23% EyeD/HeadL, 34% NarEye/HeadL, 25% Interorb/HeadL, 13% SnW/HeadL.

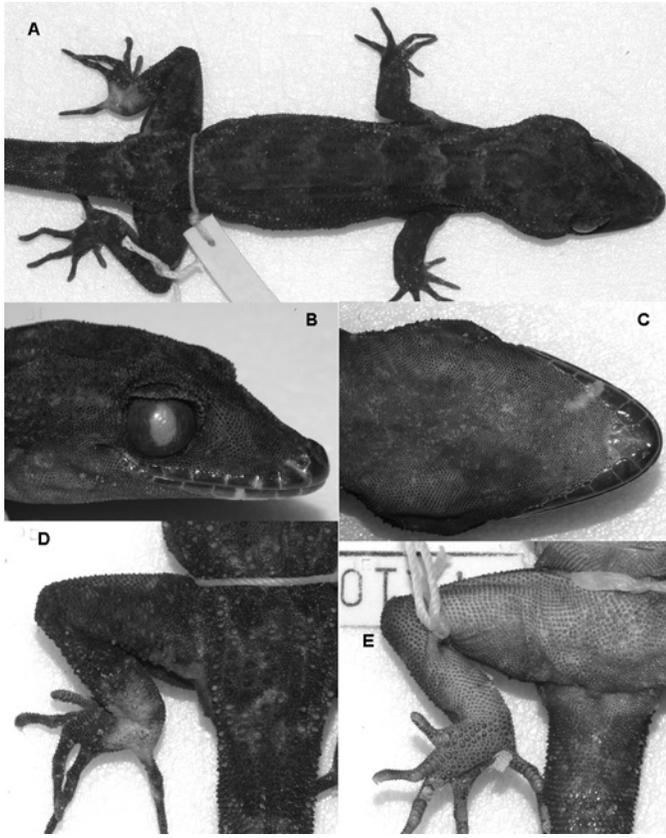


FIGURE 26. Holotype of *Nactus amplus* (BPBM 19864). (A) Dorsal view of entire body, (B) dorsolateral view of snout, (C) ventral view of head, (D) dorsal view of pelvis and thigh, and (E) ventral view of pelvis and thigh. (Photographs by M. Hagemann, BPBM.)

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 two-thirds and slightly depressed on its mid-posterior half; 4 large supralabials (right) and 4 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 3 granular loreal scales, upper largest. Supranasals moderate sized, rounded posteriorly, anteriorly touching on midline, posteriorly granular scales fill midline space created by rounded corners. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large, pentagonal mental and small postmentals (Postm = 12) and no genial scale between postmental and first supralabial. Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach ventrolaterally to near edge of venter, 18 entire rows (DorsTub), and to mid-laterally on neck; 31 tubercles per row (TubRow); 10 rows

transversely between hindlimbs (TubHip). Hindlimb with tubercles on upper and lower limbs (TubHindl = 2), and tubercles moderately abundant fore and aft (TubDens = 1). Tail anteriorly with tubercle rows dorsally, laterally, and slightly overlapping onto ventral surface. Tail ventrally with uniform small smooth scales (Subcaud = 0). Pair of cloacal spurs (CloacS) on right and left; distal edge smooth (CSTip = 0). Ventral scales from chin to vent small, granular to tuberculate. No precloacal pores. Forefoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 17 lamellae beneath fourth digit (4FingLm), 5 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 22 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as row of greatly enlarged scales.

Coloration in life not reported. In alcohol, dorsally and laterally background dusky medium brown with dark-brown transverse bars on neck, trunk, and tail; snout to occiput with dark scattered mottling; no distinct nape mark, cervical and trunk transverse bars darker laterally but continuous across midline, although lighter shade of dark brown, 4 trunk bars, none with light or dark borders, 2 dark sacral bars narrower than trunk ones, and caudal bars darker and uniformly broad. Face with unicolor loreal area, dark-brown labials with faint and narrow light-brown sutures, faint dark-brown postorbital stripe. Venter, chin, and throat medium brown, lightening posteriorly.

ETYMOLOGY. The Latin *amplus* refers to “large.” This population contains the largest known adults in the genus *Nactus*.

VARIATION. Adult females range between 75.5 and 82.1 mm SVL, adult male 67.9 mm SVL; the smallest individual in the sample is an immature female of 66.7 mm SVL. For adults, TrunkL/SVL 41.3%, 39%–44%; HeadL/SVL 28.4%, 27%–30%; HeadW/SVL 18.8%, 17%–20%; HeadW/HeadL 64.8%, 62%–69%; EyeD/SVL 7.1%, 7%–9%; EyeD/HeadL 24.9%, 23%–28%; NarEye/HeadL 32.8%, 31%–34%; Interorb/HeadL 25.6%, 24%–27%; SnW/HeadL 13.1%, 12%–13%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (4, 3–4) and infralabials (3, 3–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and small to moderately large postmentals (Postm = 12, 6–24) and usually no genial scale between postmental and first supralabial (0, 0–2 PmLab); dorsally, trunk with 17, 14–20 (DorsTub) enlarged tubercles transversely on dorsum and with 29, 27–32 tubercles (TubRow) longitudinally along trunk; 10, 8–10 tubercle rows transversely between hindlimbs (TubHip). Enlarged tubercles on crus and femur (TubHindl = 2). Tail with small uniform scales dorsally and laterally, ventrally typically with uniform, small keeled smooth (Subcaud = 1). Usually, pair of cloacal spurs (2, 2–3 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and

abdomen. Precloacal pores, male 14, females usually none, 0–11. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 \approx 5 > 1$; 19, 18–21 lamellae beneath fourth digit (4FingLm), 5, 5–7 scale rows on palm; hindfoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 23, 23–25 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, color and pattern match the general description of the holotype.

DISTRIBUTION. Like its congener *N. modicus*, *N. amplus* occurs on two island banks separated by a deep marine channel in extreme eastern Louisiade Archipelago of Milne Bay Province, Papua New Guinea, occurring on both Sudest Island and Rossel (Yela) Island (samples 46, 48; Figure 22).

Nactus chrisaustini, new species

Milne Bay Pygmy Slender-toed Gecko

HOLOTYPE. LSUMZ 123550, adult male from Look-out “Duabo” Pini Range, $10^{\circ}25.071'S$ $150^{\circ}18.413'E$, 359 m asl, Milne Bay Province, Papua New Guinea, collected by Christopher C. Austin on 12 August 2006 (Figure 27).

PARATYPES. Adult males, LSUMZ 123532, from Alotau, Napatana Lodge grounds, $10^{\circ}18.353'S$ $150^{\circ}26.231'E$, 6 m asl, Milne Bay Province, Papua New Guinea, collected by Christopher C. Austin on 7 August 2006, and LSUMZ 123535, with same collecting data as holotype; adult females, LSUMZ 123533–534 from Takwatakawai village, $10^{\circ}19.537'S$ $150^{\circ}02.259'E$, 142 m asl, collected by Christopher C. Austin on 15–16 August 2006; adult female, MCZ R146098, from Alotau, collected by Fred Parker on 19 October 1974.

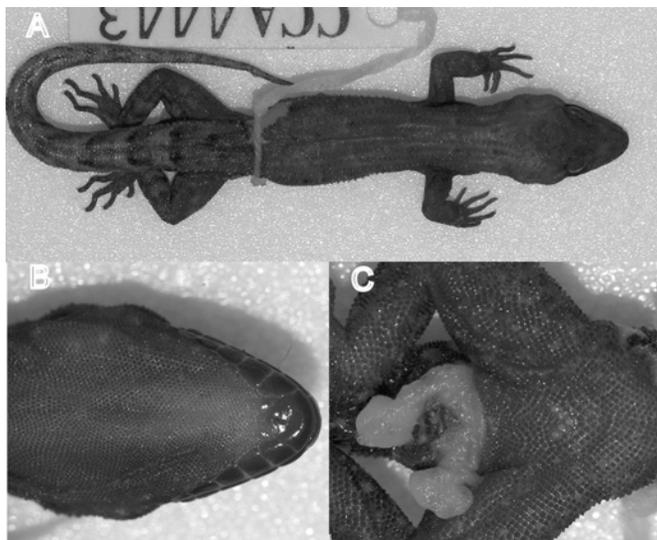


FIGURE 27. Holotype of *Nactus chrisaustini* (LSUMZ 123550). (A) Dorsal view of entire body, (B) ventral view of head, and (C) ventral view of pelvis and thigh. (Photographs by G. Zug.)

DEFINITION. A bisexual taxon of geckos (Gekkoniinae) of small adults (♀♀ 40–45 mm, ♂♂ 31–43 mm SVL) with smooth subcaudals, moderate-sized postmental scales (14–24, median 17), occasional postmental-infralabial (PmLab = 0–1, median 0.5) contact, moderate number of dorsal tubercle rows (12–15) and moderate number of tubercles (27–34, usually ≥ 29) in parasagittal row (TubRow), tubercles absent on dorsal surface of thigh and crus, and precloacal pores (5, 4–7) in males, females lack pores (0). Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 43.3.0 mm SVL, 46 mm tail length, 17.7 mm TrunkL, 17.1 mm SnForel, 11.5 mm HeadL, 7.5 mm HeadW, 5.9 mm HeadH, 2.7 mm EyeD, 3.4 mm NarEye, 2.8 mm Interorb, 1.8 mm SnW. Body proportions: 41% TrunkL/SVL, 40% SnForel/SVL, 27% HeadL/SVL, 17% HeadW/SVL, 65% HeadW/HeadL, 6% EyeD/SVL, 24% EyeD/HeadL, 30% NarEye/HeadL, 24% Interorb/HeadL, 16% 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 depressed on its mid-posterior half; 3 large supralabials (right) and 3 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 2 granular loreal scales (right and left), upper largest. Supranasals moderate sized, rounded posteriorly, anteriorly touching on midline, posteriorly granular scales fill midline space created by rounded corners. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large, pentagonal mental and moderate postmentals (Postm = 16) and no genial scale between postmental and first supralabial. Dorsum of neck and trunk with rows of enlarged tubercles from nape onto tail; on trunk rows reach laterally, 13 entire rows (DorsTub), and laterally on neck; 27 tubercles per row (TubRow); 9 rows transversely between hindlimbs (TubHip). Forelimbs and hindlimbs without tubercles on upper and lower limbs (TubHindl = 0). Tail anteriorly with short row tubercle dorsolaterally and slightly overlapping onto ventral surface. Tail ventrally with uniform small smooth scales (Subcaud = 1), slightly larger than lateral and dorsal scales. Pair of cloacal spurs (CloacS) on right and left; distal edge irregular (CSTip = 1). Ventral scales from chin to vent small, granular to tuberculate. Precloacal pores 4. Forefoot with narrow digits, their lengths $3 \approx 4 > 2 > 5 > 1$; 12 lamellae beneath fourth digit (4FingLm), 5 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 17 lamellae beneath fourth digit (4ToeLm); lamellae of first digit do not extend onto sole of foot.

Coloration in life not reported. In alcohol, background medium brown dorsally and laterally. Top of head with diffuse dark-brown preorbital chevron with cream edging anteriorly snout to occiput; supraorbital skin dark brown, otherwise dorsum medium brown; no preorbital stripe, diffuse postorbital one; supra- and infralabial scales dark brown with narrow white edges at sutures; posteriorly, lower temporal area with

small white spots that extend to forearm and ventrolaterally on chest area. Dorsally, neck and trunk to base of tail with dark-brown, ill-defined transverse bars cream edged posteriorly, separated on midline by brown of ground color, becoming distinctly chevron-like on base of tail. Forelimb uniform tan above, lighter below; hindlimbs with brown background and cream dorsolateral stripe on thigh, mottled below; crus with 2 dark transverse bars separated by cream. Venter from chin to vent uniform brown; underside of tail dark brown with numerous irregular cream to white spots.

ETYMOLOGY. The specific name *chrisaustini* recognizes the discoverer, Christopher C. Austin, of this diminutive species. The proposal of this name also recognizes his continuing research into the relationships and biology of the New Guinea herpetofauna and our friendship.

VARIATION. Females and males display slight metric differences (adult ♀♀ 41.9, 39.6–45.1 mm; adult ♂♂ 37.8, 31.4–43.3 mm SVL), although sharing similar proportions (total adult sample): TrunkL/SVL 42.4%, 40%–45%; HeadL/SVL 26.8%, 26%–29%; HeadW/SVL 17.1%, 16%–19%; HeadW/HeadL 63.6%, 61%–67%; EyeD/SVL 6.4%, 6%–8%; EyeD/HeadL 23.9%, 21%–30%; NarEye/HeadL 35.1%, 30%–43%; Interorb/HeadL 27.8%, 24%–40%; SnW/HeadL 15.8%, 15%–17%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (3, 3–4) and infralabials (3, 3–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and small to moderate to large postmentals (Postm = 17, 14–24) and variably genial scale between postmental and first supralabial (0.5, 0–1 PmLab); dorsally, trunk with 14, 12–15 (DorsTub) enlarged tubercles transversely on dorsum and with 30, 27–34 tubercles (TubRow) longitudinally along trunk; 9, 8–10 tubercle rows transversely between hindlimbs (TubHip). Usually, no enlarged tubercles on crus and femur (TubHindl = 0, 0–2). Tail with small uniform scales dorsally and laterally, ventrally with uniform, small smooth scales (Subcaud = 1). Usually, pair of cloacal spurs (2, 1–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 5, 4–7, females 0. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 \approx 5 > 1$; 14, 12–14 lamellae beneath fourth digit (4FingLm), 4.5, 4–5 scale rows on palm; hindfoot with narrow digits, their lengths typically $3 \approx 4 > 2 \approx 5 > 1$; 17.5, 17–19 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, color and pattern match the general description of the holotype. The dorsal trunk pattern of spots varies from faded to dark and ranges from 5 to 6 pairs from between shoulders to sacrum.

DISTRIBUTION. On the Milne Bay mainland, Papua New Guinea, in the forest of the southern peninsula. The Alotau locality is assumed to be a base of operation rather than a precise collecting locality (samples 49, 51, 54; Figure 22).

Nactus notios, new species

Southern Mountains Slender-toed Gecko

HOLOTYPE. LSUMZ 123547, adult male from oil palm plantation, west of Alotau, 10°23.957'S 150°5.497'E, 38 m asl, Milne Bay Province, Papua New Guinea, collected by Christopher C. Austin on 10 August 2006 (Figure 28).

PARATYPES. LSUMZ 123551–553, adult females, LSUMZ 123554–558, adult males, all with the same collecting data as holotype.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with moderate to large adults (♀♀ 55–71 mm, ♂♂ 52–70 mm SVL) with keeled subcaudals distally and smooth subcaudals basally on tail, moderate to large postmental scales (12–24, median 18), occasional postmental-infralabial (PmLab = 0–1, median 0) contact, moderate number of dorsal tubercle rows (14–19) and moderate number of tubercles (25–33, usually ≥ 29) in parasagittal row (TubRow), tubercles usually present on dorsal surface of thigh and crus, and precloacal pores (13, 10–15) in males, females lack pores (0). Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 58.2 mm SVL, 74 mm tail length (nearly totally regenerated), 21.6 mm TrunkL, 23.9 mm SnForel, 15.4 mm HeadL, 9.4 mm HeadW, 7.1 mm HeadH, 3.6 mm EyeD, 4.8 mm NarEye, 4.0 mm Interorb, 2.6 mm SnW. Body proportions: 37% TrunkL/SVL, 41% SnForel/SVL, 27% HeadL/SVL, 16% HeadW/SVL, 61% HeadW/HeadL, 6% EyeD/SVL, 23% EyeD/HeadL, 31% NarEye/HeadL, 26% Interorb/HeadL, 17% SnW/HeadL.

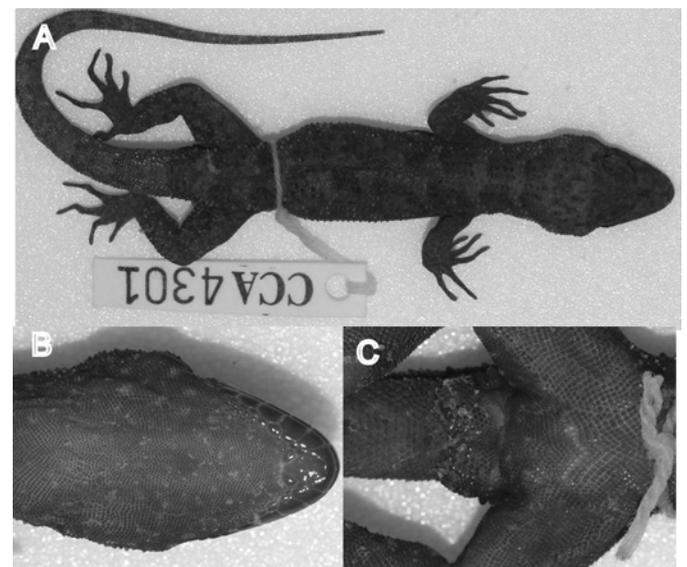


FIGURE 28. Holotype of *Nactus notios* (LSUMZ 123547). (A) Dorsal view of entire body, (B) ventral view of head, and (C) ventral view of pelvis and thigh. (Photographs by G. Zug.)

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 two-thirds and slightly depressed on its mid-posterior half; 3 large supralabials (right) and 4 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 2 granular loreal scales, upper largest. Supranasals moderate sized, rounded posteriorly, anteriorly touching on midline, posteriorly granular scales fill midline space created by rounded corners. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large, pentagonal mental and modest postmentals (Postm = 14) and single row of genial scales (anteriormost largest) between postmental and first supralabial. Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach ventrolaterally to near edge of venter, 18 entire rows (DorsTub), and to mid-laterally on neck; 27 tubercles per row (TubRow); 10 rows transversely between hindlimbs (TubHip). Hindlimb with numerous tubercles on dorsal surface of upper and lower limbs (TubHindl = 2), and tubercles moderately abundant fore and aft (TubDens = 1). Tail anteriorly with tubercle rows dorsally, laterally, and slightly overlapping onto ventral surface. Tail ventrally with mix of small keeled and smooth scales basally (Subcaud = 2). Pair of cloacal spurs (CloacS) on right and left; distal edge irregular (CSTip = 1). Ventral scales from chin to vent small, granular to tuberculate. Precloacal pores 13. Forefoot with narrow digits, their lengths $3 \approx 4 > 2 > 5 > 1$; 22 lamellae beneath fourth digit (4FingLm), 7 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $3 \approx 4 > 5 > 2 > 1$; 18 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as row of enlarged scales.

Coloration in life not reported. In alcohol, background medium brown dorsally, laterally, and ventrally. Top of head with small dark-brown marks on snout to occiput and irregular-edged prefrontal stripe; narrow dark-brown preorbital stripe in loreal area and broad cream postorbital stripe bordered above and below by dark brown to above tympanum; supralabials medium brown with cream edges anteriorly and posteriorly, giving broad barred appearance, infralabials similarly colored. Dorsally, neck and trunk to base of tail with paired dark-brown blotches, separated on midline by brown of ground color continuing to base of tail. Forelimb brown above and lightly mottled with dark brown above, unicolor below; hindlimbs with medium-brown background irregularly marked with dark brown and some near-white tubercles. Venter from chin to vent uniform medium brown.

ETYMOLOGY. The specific name *notios* is a Greek adjective for “southern, wet, rainy” and refers to the location of this population in the southern peninsula and its mountains of mainland Milne Bay.

VARIATION. Females and males display slight metric differences (adult ♀♀ 63.9, 55.4–70.9 mm; adult ♂♂ 60.0,

52.1–70.1 mm SVL), although sharing similar proportions (total adult sample): TrunkL/SVL 41.6%, 37%–45%; HeadL/SVL 27.0%, 26%–28%; HeadW/SVL 17.0%, 16%–18%; HeadW/HeadL 63.2%, 58%–67%; EyeD/SVL 6.2%, 5%–7%; EyeD/HeadL 23.1%, 20%–26%; NarEye/HeadL 32.1%, 30%–41%; Interorb/HeadL 25.6%, 23%–28%; SnW/HeadL 14.8%, 13%–17%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (4, 3–5) and infralabials (4, 3–5) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and moderate to large postmentals (Postm = 18, 12–24) and genial scale occasionally between postmental and first supralabial (0, 0–1 PmLab); dorsally, trunk with 17, 14–19 (DorsTub) enlarged tubercles transversely on dorsum and with 30, 25–33 tubercles (TubRow) longitudinally along trunk; 10, 8–10 tubercle rows transversely between hindlimbs (TubHip). Enlarged tubercles on crus and femur (TubHindl = 2). Tail with small uniform scales dorsally and laterally and mix of small keeled and smooth scales basally (Subcaud = 2). Usually, pair of cloacal spurs (2, 1–3 CloacS) on each side. Ventral scales from chin to vent small, granular, and unicolorate, somewhat larger on chest and abdomen. Cloacal pores, males 10–15, females 0. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 \approx 5 > 1$; 17, 14–22 lamellae beneath fourth digit (4FingLm), 7, 5–9 scale rows on palm; hindfoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 22, 18–24 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, color and pattern match the general description of the holotype. The cream postorbital stripe may be absent in some individuals. The dorsal trunk pattern of paired dorsal blotches is distinct in all individuals and ranges from 5 to 6 pairs from between shoulders to sacrum. If tail is unregenerated, it is regularly dark banded.

DISTRIBUTION. Forests of the southern peninsula of the Milne Bay mainland, Papua New Guinea (samples 51, 53, 54; Figure 22).

Nactus erugatus, new species

Milne Bay Smooth-tailed Slender-toed Gecko

HOLOTYPE. BPBM 15448, adult male from Duabo, Pini Range, 10°06'S 151°15'E, 300 m, Milne Bay Province, Papua New Guinea, collected by Fred Kraus on 1 May 2002 (Figure 29).

PARATYPES. Adult females, BPBM 15449, with same collecting data as holotype, and BPBM 15451–452 from Owen Stanley Range, Mount Pekopekowan, Garden Camp, 10°17.104'S, 150°10.930'E, 330 m, Milne Bay Province, Papua New Guinea, collected by Fred Kraus and I. Bigilale on 7 May 2002; adult males, BPBM 15443 from Bwaona River, Alotau,

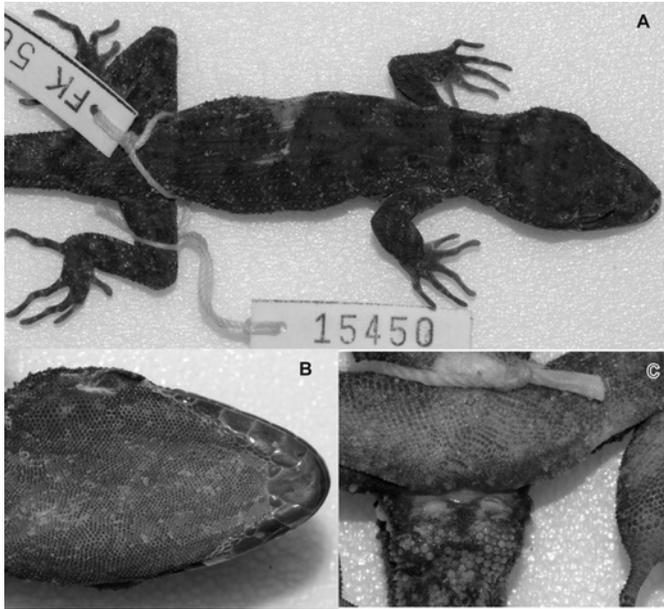


FIGURE 29. Paratype of *Nactus erugatus* (BPBM 15450). (A) Dorsal view of entire body, (B) ventral view of head, and (C) ventral view of pelvis and thigh. (Photographs by G. Zug.)

10°30'14"S, 150°18'50"E, 90 m, Milne Bay Province, Papua New Guinea, collected by Fred Kraus on 7 April 2002, and BPBM 15450 from Mount Pekopekowan, Garden Camp, 10°17.104'S, 150°10.930'E, 330 m, Milne Bay Province, Papua New Guinea, collected by Fred Kraus and I. Bigilale on 7 May 2002.

DEFINITION. A bisexual taxon of geckos (Gekkoniinae) with large adults (♀ 66–72 mm, ♂ 59–69 mm SVL) with smooth subcaudals, moderate-sized postmental scales (10–20, median 14), no or slight postmental-infralabial (PmLab = 0–1, median 0) contact, moderate number of dorsal tubercle rows (15–18) and moderate number of tubercles (28–34, usually ≥ 29) in parasagittal row (TubRow), tubercles usually present on dorsal surface of thigh and crus, and precloacal pores 12–14 in males and 6–12 in females. Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 68.2 mm SVL, tail length not recorded, 27.0 mm TrunkL, 29.0 mm SnForel, 19.6 mm HeadL, 12.2 mm HeadW, 8.7 mm HeadH, 6.1 mm EyeD, 6.4 mm NarEye, 5.2 mm Interorb, 2.8 mm SnW. Body proportions: 39% TrunkL/SVL, 41% SnForel/SVL, 28% HeadL/SVL, 18% HeadW/SVL, 62% HeadW/HeadL, 7% EyeD/SVL, 26% EyeD/HeadL, 33% NarEye/HeadL, 27% Interorb/HeadL, 14% 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 two-thirds and slightly depressed on its mid-posterior half; 4 large supralabials (right) and 3 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of

respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 2 granular loreal scales (right, 3 left), upper largest. Supranasals moderate sized, rounded posteriorly, anteriorly touching on midline, posteriorly granular scales fill midline space created by rounded corners. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large, pentagonal mental and moderately large postmentals (Postm = 18) and no genial scale between postmental and first supralabial. Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach ventrolaterally to near edge of venter, 18 entire rows (DorsTub), and to mid-laterally on neck; 30 tubercles per row (TubRow); 10 rows transversely between hindlimbs (TubHip). Hindlimb with tubercles on upper and lower limbs (TubHindl = 2), and tubercles moderately abundant fore and aft (TubDens = 1). Tail anteriorly with tubercle rows dorsally, laterally, and slightly overlapping onto ventral surface. Tail ventrally with uniform small smooth scales (Subcaud = 1). Pair of cloacal spurs (CloacS) on right and left; distal edge smooth (CSTip = 0). Ventral scales from chin to vent small, granular, and most bicarinate. Precloacal pores 12. Forefoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 17 lamellae beneath fourth digit (4FingLm), 5 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 22 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as row of greatly enlarged scales.

Coloration in life not reported. In alcohol, background medium brown dorsally and laterally. Top of head with scattered small dark-brown spots from snout to occiput; supralabials medium brown with light-brown sutures, infralabials similarly colored. Dorsally, with dark-brown, transverse markings, nape bar narrow crescent, cervical broad continuous bar, from axilla to inguina series of 6 pairs of uniformly dark blotches well separated medially, posterior sacral and first caudal dark-brown, somewhat V-shaped marks; fore- and hindlimbs irregularly marked with dark-brown, irregularly shaped spots. Venter unicolor medium brown.

ETYMOLOGY. The specific name *erugatus* derives from the Latin *erugo*, “to take wrinkles from or smooth,” and refers to the smooth or keel-free subcaudals of this taxon.

VARIATION. Females and males display slight metric differences (adult ♀♀ 69.7, 66.2–72.2 mm; adult ♂♂ 63.1, 59.0–69.2 mm SVL), although sharing similar proportions (total adult sample): TrunkL/SVL 41.6%, 38%–45%; HeadL/SVL 27.5%, 26%–28%; HeadW/SVL 17.6%, 16%–18%; HeadW/HeadL 63.9%, 62%–66%; EyeD/SVL 6.9%, 6%–7%; EyeD/HeadL 25.0%, 23%–25%; NarEye/HeadL 32.3%, 31%–33%; Interorb/HeadL 25.6%, 23%–27%; SnW/HeadL 14.5%, 14%–15%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (4, 3–4) and infralabials (3, 3–4) in front of anterior edge of orbit, first supra- and

infralabial largest of respective series. Chin with large trapezoidal mental and small to moderate postmentals (Postm = 14, 10–20) and usually no genial scale between postmental and first supralabial (0, 0–1 PmLab); dorsally, trunk with 17, 15–18 (DorsTub) enlarged tubercles transversely on dorsum and with 30, 28–34 tubercles (TubRow) longitudinally along trunk; 10, 8–10 tubercle rows transversely between hindlimbs (TubHip). Enlarged tubercles on crus and femur (TubHindl = 2). Tail with small uniform scales dorsally and laterally, ventrally typically with uniform, small smooth scales (Subcaud = 0). Usually, pair of cloacal spurs (2, 1–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 12–14, females 6–12. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 \approx 5 > 1$; 18, 17–19 lamellae beneath fourth digit (4FingLm), 5, 4–7 scale rows on palm; hindfoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 22, 19–23 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, color and pattern match the general description of the holotype.

DISTRIBUTION. Southeastern terminus of the Owen Stanley Range in Milne Bay Province, Papua New Guinea (samples 51, 54; Figure 22).

Nactus alotau, new species

Southern Forest Slender-toed Gecko

HOLOTYPE. BPBM 15849, adult male from Papua New Guinea, Milne Bay Province, Alotau, -10.3157° 150.4588° , collected by Fred Kraus on 13 August 2002 (Figure 30).

PARATYPES. Adult females, BPBM 15852, from Halowia, 15.8 km east of Alotau, collected by Fred Kraus on 23 September 2002, LSUMZ 93326, Alotau, Napatana Lodge, collected by Christopher C. Austin on 9 August 2006, MCZ 146097–098, Alotau, collected by Fred S. Parker on 19 October 1974, USNM 159816, Milne Bay, collected by R. M. Roecker on 3 March 1944, and adult males, AMS R124906 from Koea Bule Mission, $10^{\circ}18'S$ $150^{\circ}24'E$, near Alotau, collected by

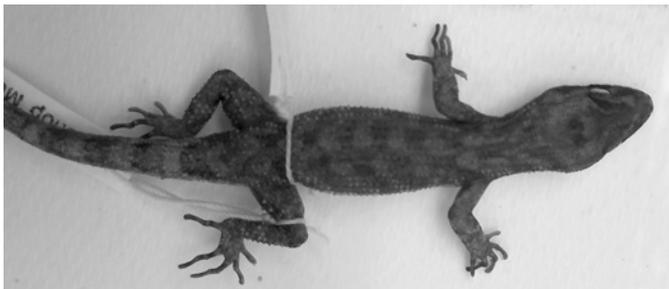


FIGURE 30. Holotype of *Nactus alotau* (BPBM 15849). Dorsal view of entire body. (Photograph by M. Hagemann, BPBM.)

G. Mengden on 14 August 1987, BPBM 15663, same data as holotype, 15851 from Halowia, 15.8 km east of Alotau, collected by Fred Kraus on 23 September 2002; all localities in Milne Bay Province, Papua New Guinea.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with moderate to large adults (♀♀ 44–67 mm SVL, ♂♂ 43–66 mm SVL) with keeled subcaudals, usually moderate postmental scales (6–22, median 14), occasional postmental-infralabial contact (PmLab 0–2, 0), moderate number of dorsal tubercle rows (6–20) and moderate number of tubercles (21–46, usually ≥ 27) in parasagittal row (TubRow), tubercles present on dorsal surface of thigh and crus (uncommonly on only crus), and precloacal pores (8, 0–13) in males, females usually lack pores (0, 0–9). Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 55.2 mm SVL, 22.2 mm TrunkL, 22.8 mm SnForel, 14.3 mm HeadL, 9.4 mm HeadW, 6.3 mm HeadH, 3.7 mm EyeD, 4.8 mm NarEye, 3.7 mm Interorb, 2.1 mm SnW. Body proportions: 40% TrunkL/SVL, 41% SnForel/SVL, 26% HeadL/SVL, 17% HeadW/SVL, 66% HeadW/HeadL, 7% EyeD/SVL, 26% EyeD/HeadL, 34% NarEye/HeadL, 26% Interorb/HeadL, 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 slightly depressed on its mid-posterior half; 3 large supralabials (right) and 3 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 2 granular loreal scales (right, 3 left), upper largest. Supranasals moderate sized, rounded posteriorly, anteriorly touching on midline, posteriorly bordered by granular scales. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large, pentagonal mental and moderate postmentals (Postm = 12) and no genial scale between postmental and first supralabial. Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach ventrolaterally to near edge of venter, 17 entire rows (DorsTub), and to mid-laterally on neck; 29 tubercles per row (TubRow); 10 rows transversely between hindlimbs (TubHip). Hindlimb with tubercles on upper and lower limbs (TubHindl = 2), and tubercles moderately abundant fore and aft (TubDens = 1). Tail anteriorly with tubercle rows dorsally, laterally, and slightly overlapping onto ventral surface. Tail ventrally with uniform small keeled scales (Subcaud = 0). Pair of cloacal spurs (CloacS) on right and left; distal edge irregular (CSTip = 1). Ventral scales from chin to vent small, granular to tuberculate. Precloacal pores 9. Forefoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 14 lamellae beneath fourth digit (4FingLm), 4 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $4 > 3 > 5 > 2 > 1$; 18 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as row of greatly enlarged scales.

Coloration in life not reported. In alcohol, background tan dorsally and laterally. Top of head with few thin, dark brown

irregularly shaped marks on snout to occiput; distinct dark-brown preorbital stripe continuing behind eye as broader post-orbital stripe to above tympanum; supralabials medium brown with cream edges anteriorly and posteriorly, giving broad barred appearance, infralabials similarly colored. Dorsally, neck and trunk to base of tail with dark-brown, ill-defined transverse bars; dark-brown transverse bars on base of tail with posterior cream borders. Forelimb uniform tan above, lighter below; hindlimbs with tan background and dark-brown transverse bars on thigh, near white below; crus with 2 dark transverse bars separated by tan. Venter from chin to vent light tan.

ETYMOLOGY. The specific name derives from the principal mainland town, Alotau, of Milne Bay Province and is used as a noun in apposition.

VARIATION. Females and males display slight metric differences (adult ♀♀ 58.0, 44.0–67.2 mm; adult ♂♂ 55.5, 42.8–66.3 mm SVL), although sharing similar proportions (total adult sample): TrunkL/SVL 42.0%, 34%–49%; HeadL/SVL 26.9%, 25%–39%; HeadW/SVL 17.6%, 16%–20%; HeadW/HeadL 65.6%, 47%–79%; EyeD/SVL 6.6%, 5%–8%; EyeD/HeadL 24.6%, 18%–31%; NarEye/HeadL 31.0%, 19%–35%; Interorb/HeadL 27.2%, 21%–36%; SnW/HeadL 14.5%, 10%–17%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (4, 3–4) and infralabials (3, 2–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and moderate postmentals (Postm = 14, 6–22) and occasional genial scale between postmental and first supralabial (0, 0–2 PmLab); dorsally, trunk with 14, 6–22 (DorsTub) enlarged tubercles transversely on dorsum and with 27, 21–46 tubercles (TubRow) longitudinally along trunk; 10, 7–10 tubercle rows transversely between hindlimbs (TubHip). Enlarged tubercles on crus and femur (TubHindl = 2, uncommonly crus only). Tail with small uniform scales dorsally and laterally, ventrally variable with uniform, small keeled scales (Subcaud = 0). Usually, pair of cloacal spurs (2, 1–3 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 0–13 usually present, females usually lack pores, 0–9. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 \approx 5 > 1$; 18, 13–20 lamellae beneath fourth digit (4FingLm), 5, 4–6 scale rows on palm; hindfoot with narrow digits, their lengths $4 > 3 > 5 > 2 > 1$ or $3 \approx 4 > 2 \approx 5 > 1$; 22, 17–25 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, color and pattern match the general description of the holotype. The dorsal trunk pattern of transverse bars varies from faded to dark; in some the dark bars are distinctly edged posteriorly in cream and range from 5 to 6 bars between shoulders to sacrum. Forelimbs are usually uniformly medium brown; hindlimbs (thigh) are commonly mottled with dark brown dorsally and uniform light brown to cream posteriorly.

DISTRIBUTION. Individuals of *N. alotau* occur widely in mainland Milne Bay and westward along the south coast to and through the Central Province. This wide occurrence presumably reflects its tolerance and success in adapting to disturbed forest habitats (samples 49, 50, 51, 52, 53, 54, 55, 57; Figure 22).

***Nactus heteronotus* (Boulenger, 1885) Central Savanna Slender-toed Gecko**

Heteronota fasciata Macleay, 1878:100 [type locality: “Hall Sound”].

Gymnodactylus heteronotus Boulenger, 1885:41. Substituted name for the homonym *Heteronota fasciata* Macleay.

HOLOTYPE. AMS R31934, no additional data than type locality, although collector possibly Macleay.

DEFINITION. A bisexual taxon of geckos (Gekkoniinae) of small to moderate adults (♀♀ 39–47 mm, ♂♂ 37–48 mm SVL) with keeled subcaudals, usually moderate postmental scales (6–20, median 12), no postmental-infralabial contact (PmLab 0), low number of dorsal tubercle rows (11–14) and moderate number of tubercles (19–32, median 24) in parasagittal row (TubRow), tubercles present on dorsal surface of thigh and crus (uncommonly on only crus), and few precloacal pores in males (5, 0–7), females usually lack pores (0, 0–1). Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. A poorly preserved, deteriorating specimen, unsexed, presumably immature individual of 35 mm SVL, tail length not recorded, TrunkL not recorded, SnForel not recorded, 10.7 mm HeadL, 6.5 mm HeadW, HeadH not recorded, 2.7 mm EyeD, NarEye not recorded, Interorb not recorded, SnW not recorded. Body proportions: TrunkL/SVL unknown, SnForel unknown, 31% HeadL/SVL, 19% HeadW/SVL, 61% HeadW/HeadL, 8% EyeD/SVL, 25% EyeD/HeadL, 29% NarEye/HeadL, 31% Interorb/HeadL, 16% 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 slightly depressed on its mid-posterior half; 3 large supralabials (right) and 3 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 3 granular loreal scales (right, 3 left), upper largest. Supranasals moderate sized, rounded posteriorly, separated on midline by single, slightly enlarged granular scales and posteriorly bordered by small granular scales. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large, pentagonal mental and moderate postmentals (Postm = 16) and no genial scale between postmental and first supralabial. Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach ventrolaterally to near edge of venter, 17 entire rows (DorsTub), and to mid-laterally on neck; ~42 tubercles per row (TubRow); 7 rows transversely between hindlimbs (TubHip). Hindlimb

with tubercles on upper and lower limbs (TubHindl = 2), few tubercles on thigh, moderately abundant on crus. Tail anteriorly with tubercle rows dorsally; broken just posterior to vent and missing, laterally, and slightly overlapping onto ventral surface. Regenerated tail ventrally with uniform small keeled scales (Subcaud = 0). Pair of cloacal spurs (CloacS) on right and left; distal edge irregular (CSTip = 1). Ventral scales from chin to vent small, granular to tuberculate. Forefoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 14 lamellae beneath fourth digit (4FingLm), 4 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $4 > 3 > 5 > 2 > 1$; 18 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as row of greatly enlarged scales.

Coloration in life not reported. In alcohol, background tan dorsally and laterally. Top of head with few thin, dark-brown irregularly shaped marks on snout to occiput; distinct dark-brown preorbital stripe continuing behind eye as broader post-orbital stripe to above tympanum; supralabials medium brown with cream edges anteriorly and posteriorly, giving broad barred appearance, infralabials similarly colored. Dorsally, neck and trunk to base of tail with dark-brown, ill-defined transverse bars; dark-brown transverse bars on base of tail with posterior cream borders. Forelimb uniform tan above, lighter below; hindlimbs with tan background and dark-brown transverse bars on thigh, near white below; crus with 2 dark transverse bars separated by tan. Venter from chin to vent light tan. (Derived from Yule Island specimen, USNM 325082; Figure 31.)

ETYMOLOGY. Boulenger did not explain his choice of *heteronotus* as a replacement name, presumably different dorsal trunk scales from the Greek *heteros* (“other,” “different”) and *notos* (“back”).

VARIATION. Females and males display slight metric differences (adult ♀♀ 43.3, 38.5–47.1 mm; adult ♂♂ 42.1, 37.2–47.7 mm SVL), although sharing similar proportions (total adult sample): TrunkL/SVL 42.7%, 33%–49%; HeadL/SVL 26.2%, 20%–28%; HeadW/SVL 18.5%, 14%–21%; HeadW/HeadL 70.9%, 62%–83%; EyeD/SVL 6.4%, 5%–9%; EyeD/HeadL 24.8%, 20%–36%; NarEye/HeadL 31.4%, 28%–36%; Interorb/HeadL 30.0%, 22%–44%; SnW/HeadL 16.2%, 14%–24%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (3, 3–4) and infralabials (3, 2–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and moderate postmentals (Postm = 12, 6–20) and with no genial scale between postmental and first supralabial (0 PmLab); dorsally, trunk with 13, 11–14 (DorsTub) enlarged tubercles transversely on dorsum and with 24, 19–32 tubercles (TubRow) longitudinally along trunk; 8, 8–9 tubercle rows transversely between hindlimbs (TubHip). Enlarged tubercles on crus and femur variable (TubHindl = 1 or 2) and possibly

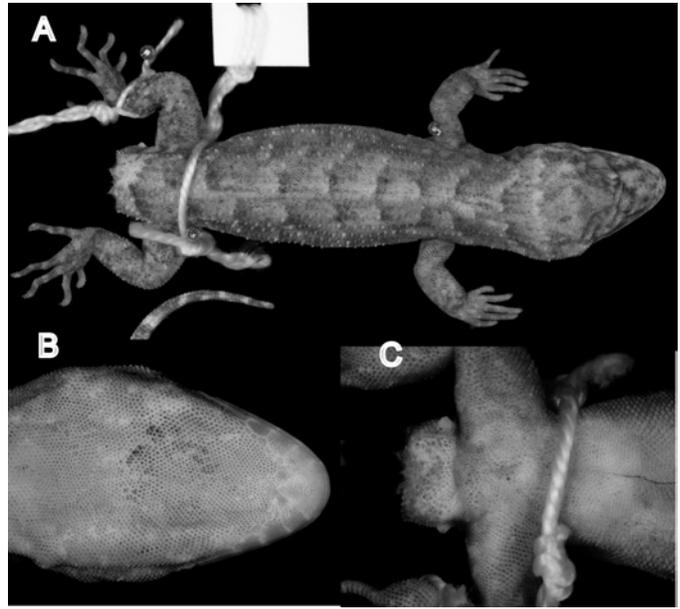


FIGURE 31. Topotype of *Nactus heteronotus* (USNM 325082). (A) Dorsal view of entire body, (B) ventral view of head, and (C) ventral view of pelvis and thigh. (Photographs by E. Langan, USNM.)

sexually dimorphic as 23% of males have tubercles on only crus compared to 8% of the females. Tail with small uniform scales dorsally and laterally, ventrally variable with uniform, small keeled scales (Subcaud = 0). Usually, pair of cloacal spurs (2, 0–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 3–7, females usually lack pores, 0–1. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 \approx 5 > 1$; 14, 11–15 lamellae beneath fourth digit (4FingLm), 6, 4–7 scale rows on palm; hindfoot with narrow digits, their lengths $4 > 3 > 5 > 2 > 1$ or $3 \approx 4 > 2 \approx 5 > 1$; 18, 16–20 lamellae beneath fourth toe (4ToeLm).

Coloration in life from F. Kraus’s photo of Moresby area specimen. Dorsal background brown from snout to posterior trunk becoming brownish white. This light color evident ventrolaterally from throat to and onto tail. Top of head vaguely marked with darker-brown moderately broad canthal white stripe onto anterior edge of eye, bordered below by white and dark-brown upper lip; moderately broad dark-brown post-orbital stripe to ear. Dorsally, trunk with 6 irregular dark-brown transverse bars extending onto base of tail. In alcohol, color and pattern match the general description of the topotype. The top of the head is usually unicolor or indistinctly mottled; the sides of the head range from unicolor to possession of distinct dark pre- and postocular stripes with broadly barred lips. The dorsal trunk pattern of transverse bars varies from faded to dark, but all bars

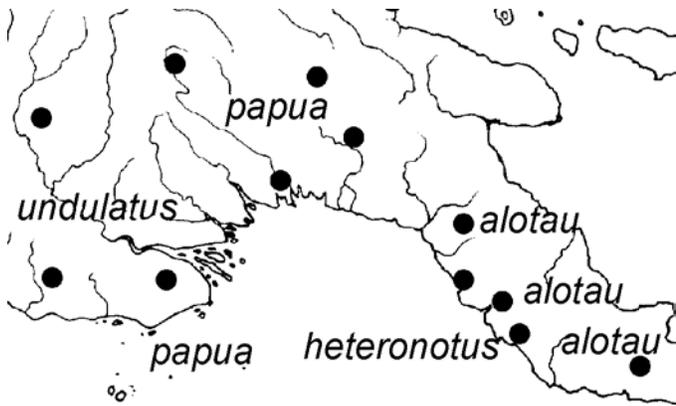


FIGURE 32. Occurrence of *Nactus* species on the south coast of Papua New Guinea. The solid circles are sample localities identified in Figure 1.

are irregularly formed without distinct borders; in some the dark bars are distinctly edged posteriorly in cream and range from 5 to 6 bars between shoulders to sacrum. Forelimbs are usually uniformly medium brown; hindlimbs (thigh) are unicolor to faintly mottled with dark brown dorsally. Underside is unicolor light brown to cream. Unregenerated tails are distinctly banded in light tan to cream and brown.

DISTRIBUTION. Individuals of *N. heteronotus* occur in the coastal savannas of the Central Province and the National Capital Province (samples 56, 58; Figure 32).

Lakemba Basin *N. alotau* population (sample 59)

COMMENTS. In 2010, Heinicke and colleagues included two uncataloged Tekadu tissue samples in their molecular analysis of *Nactus*. The two individuals were sister to one another but genetically different from one another; these individuals were sister to a pair of genetically similar *N. eboracensis* from Coen, Australia (Heinicke et al., 2010: fig. 5B). I did not locate the vouchers for the Tekadu tissue samples; hence, I have no morphological data to compare them to one another or to my small Lakemba drainage sample. My Lakemba sample (59) includes an adult male and four adult females. Aside from showing all three states of hindlimb tubercles, they are similar to one another and show no discernable differences from specimens of *N. alotau* of southeastern Papua New Guinea. Sample 59 specimens are from the lower reaches of the Lakemba River, whereas the Tekadu specimens are from Morobe Province, an upriver (mountain valley) site in the Lakemba River drainage.

DESCRIPTION. Females and male are similar in size (adult ♀♀ 56.3, 57.0–61.4 mm; adult ♂ 59.1 mm SVL) and share similar proportions (total adult sample): TrunkL/SVL 43.5%; HeadL/SVL 26.9%; HeadW/SVL 18.2%; HeadW/HeadL 67.6%; EyeD/SVL 6.0%; EyeD/HeadL 22.2%; NarEye/HeadL 31.0 %; Interorb/HeadL 25.2%; SnW/HeadL 14.4%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Large supralabials (3) and infralabials (3) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and moderate-sized postmentals (Postm = 12, 6–18) and no genial scale between postmental and first supralabial; dorsally, trunk with 14–17 (DorsTub) enlarged tubercles transversely on dorsum and with 35, 26–37 tubercles (TubRow) longitudinally along trunk; 8–10 tubercle rows transversely between hindlimbs (TubHip). Enlarged tubercles on crus and femur are variable; one individual with tubercle only on crus, another with tubercles on both thigh and crus, and three lacking hindlimb tubercles. Tail with small uniform scales dorsally and laterally, ventrally typically with uniform, small keeled scales (Subcaud = 0). Two cloacal spurs on each side. Ten precloacal pores in male, females usually lack pores (0, 0–2). Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Forefoot with narrow digits, 16–18 lamellae beneath fourth digit (4FingLm), 5–7 scale rows on palm; hindfoot with narrow digits, 20, 19–20 lamellae beneath fourth toe (4ToeLm).

Coloration in preservative, background medium brown dorsally and laterally, ventrally somewhat lighter and unicolor. Top of head with ill-defined darker-brown marks from snout to occiput; lores and temporal areas without distinct markings; supra- and infralabials dark brown with white sutures. Dorsally, neck and trunk with diffuse dark-brown cross bars and only on base of tail with cream edged chevron-like at base of tail.

Nactus papua, new species

Papuan Slender-toed Gecko

HOLOTYPE. CAS 118023, adult male from Papua New Guinea, Gulf Province, Uruu [6°53'37"S 144°52'30"E], collected by Fred Parker on 1 October 1967 (Figure 33).

PARATYPES. Adult male, CAS 118032, with same data as holotype, and adult females, MCZ 101622, 101626, USNM 192414–415, with same data as the holotype except 2 October 1967.

DEFINITION. A bisexual taxon of geckos (Gekkoninae) with moderate to large adults (♀♀ 49–64 mm, ♂♂ 55–64 mm SVL) with keeled subcaudals, usually moderate postmental scales (0–18, median 13), occasional postmental-infralabial contact (PmLab 0–4, 0), moderate number of dorsal tubercle rows (11–17) and moderate number of tubercles (23–41, usually ≥32) in parasagittal row (TubRow), tubercle presence variable on dorsal surface of thigh and crus (usually on both thigh and crus or rarely absent on both), and variable presence of precloacal pores 0–12. Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 60.1 mm SVL, 25.0 mm TrunkL, 23.5 mm SnForel, 16.6 mm HeadL, 10.3 mm HeadW, 7.9 mm HeadH, 4.4 mm EyeD, 5.1 mm NarEye, 4.2 mm Interorb, 2.5 mm SnW. Body proportions: 42% TrunkL/SVL, 39% SnForel/SVL, 28% HeadL/SVL,

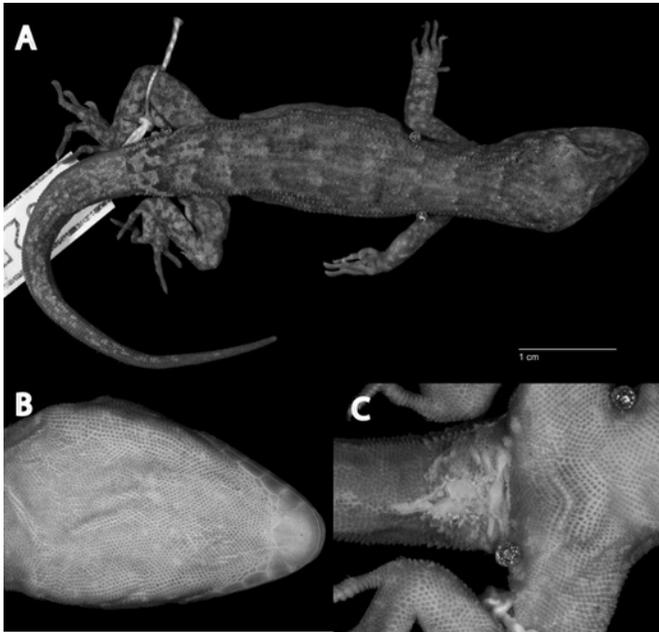


FIGURE 33. Holotype of *Nactus papua* (CAS 118023). (A) Dorsal view of entire body, (B) ventral view of head, and (C) ventral view of pelvis and thigh. (Photographs by E. Ely, CAS.)

17% HeadW/SVL, 62% HeadW/HeadL, 7% EyeD/SVL, 26% EyeD/HeadL, 31% NarEye/HeadL, 25% Interorb/HeadL, 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 slightly depressed on its mid-posterior half; 3 large supralabials (right) and 3 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 2 granular loreal scales (right, 3 left), upper largest. Supranasals moderate sized, rounded posteriorly, anteriorly touching on midline, posteriorly bordered by granular scales. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large, pentagonal mental and moderate postmentals (Postm = 10) and no genial scale between postmental and first supralabial. Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach ventrolaterally to near edge of venter, 16 entire rows (DorsTub), and to mid-laterally on neck; 31 tubercles per row (TubRow); 9 rows transversely between hindlimbs (TubHip). Hindlimb with tubercles on upper and lower limbs (TubHindl = 2), and tubercles moderately abundant fore and aft (TubDens = 1). Tail anteriorly with tubercle rows dorsally, laterally, and slightly overlapping onto ventral surface. Tail ventrally with uniform small keeled scales (Subcaud = 0). Pair of cloacal spurs (CloacS) on right and left; distal edge irregular (CSTip = 1).

Ventral scales from chin to vent small, granular to tuberculate. Preloacal pores, males 0–12, females 0–11. Forefoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 17, 15–21 lamellae beneath fourth digit (4FingLm), 6, 4–9 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $3 \approx 4 > 5 > 2 > 1$; 19–25 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as row of greatly enlarged scales.

Coloration in life not reported. In alcohol, background tan to medium brown dorsally and laterally. Snout mottled with dark-brown and white marks, crown and nuchal area with dark-brown smudge-like marks on snout to occiput; from mid neck to base of tail, series of transverse irregular edged dark-brown bars with narrow white posteriorly, dark bars become chevron-like with broader white edges. Face with indistinct white marks on lores, supra- and infralabials strongly barred with dark-brown centers and white borders, and ill-defined dark postorbital stripe bordered above and below in white. Venter from chin to vent light brown.

ETYMOLOGY. The specific name derives from the occurrence of this species in the Papuan area of Papua New Guinea adjacent to the Gulf of Papua (samples 60, 61).

VARIATION. Females and males display slight metric differences (adult ♀♀ 57.8, 49.1–64.4 mm; adult ♂♂ 59.2, 54.9–64.0 mm SVL), although sharing similar proportions (total adult sample): TrunkL/SVL 42.6%, 39%–48%; HeadL/SVL 26.9%, 25%–30%; HeadW/SVL 18.1%, 16%–21%; HeadW/HeadL 67.6%, 60%–78%; EyeD/SVL 6.7%, 6%–8%; EyeD/HeadL 25.1%, 22%–31%; NarEye/HeadL 30.8%, 27%–35%; Interorb/HeadL 26.0%, 21%–31%; SnW/HeadL 14.2%, 12%–17%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale bearing middorsal cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (3, 2–4) and infralabials (3, 2–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and usually moderate postmentals (Postm = 10, 0–18) and occasional genial scale between postmental and first supralabial (0, 0–4 PmLab); dorsally, trunk with 14, 11–17 (DorsTub) enlarged tubercles transversely on dorsum and with 33, 23–41 tubercles (TubRow) longitudinally along trunk; 9, 8–10 tubercle rows transversely between hindlimbs (TubHip). Enlarged tubercles on crus and femur variable (TubHindl = 0 or 2, i.e., usually on both thigh and crus and rarely absent on both). Tail with small uniform scales dorsally and laterally, ventrally variable with uniform, small keeled scales (Subcaud = 0). Usually, pair of cloacal spurs (2, 1–3 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Preloacal pores, present in most males 0–12 and in about half of females 0–11. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 \approx 5 > 1$; 17, 15–21 lamellae beneath fourth digit (4FingLm), 6, 4–9 scale rows on palm; hindfoot with narrow

digits, their lengths $4 > 3 > 5 > 2 > 1$ or $3 \approx 4 > 2 \approx 5 > 1$; 22, 19–25 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, color and pattern match the general description of the holotype. The dorsal trunk pattern of transverse bars varies from faded to distinct; in some the dark bars are distinctly edged posteriorly in cream and range from 5 to 6 bars between shoulders to sacrum; bars often separated, narrowly to broadly, on dorsal midline. Forelimbs usually mottled in dark brown, medium brown, and cream; hindlimbs (thigh) strikingly mottled in dark brown and cream dorsally and posteriorly; tail brightly and irregularly banded in dark brown to cream dorsally and laterally and less distinctly ventrally; venter uniform medium brown.

DISTRIBUTION. Individuals of *N. papua* occur in southern Papua from Kerema and westward to the Kikori River (samples 60, 61).

Torres Strait Islands *N. cf. papua* (sample TS)

COMMENTS. The islands of the Torres Strait have a mixture of *N. eboracensis* with smooth subcaudal scales and a New Guinea *Nactus* with keeled subcaudal scales. The New Guinea *Nactus* occurs nearly to the Cape York Peninsula, predominantly on the islands of the eastern side (Zug, 1998: fig. 5). These insular populations consist of nondimorphic adults averaging 48 mm SVL (41–59 mm SVL) with midsize postmentals (14, 6–20), all females ($n = 14$) except one lack precloacal pores, and all males ($n = 8$) except one have pores (6–10). All Torres Strait individuals possess tubercles on the thigh and crus (TubHindl = 2). Aside from smaller average SVL, these traits match closely the *N. papua* populations of the Gulf of Papua coast rather than the geographically closer *N. inundatus* populations of the Fly River delta.

DESCRIPTION. Females and males are similar in size (adult ♀♀ 47.0, 40.7–56.6 mm; adult ♂♂ 48.8, 43.4–59.3 mm SVL).

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Large supralabials (3, 3–4) and infralabials (2, 2–3) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and moderate-sized postmentals (Postm = 14, 6–20) and rarely a genial scale between postmental and first supralabial; dorsally, trunk with 13–18 (DorsTub) enlarged tubercles transversely on dorsum and with 21.5, 18–29 tubercles (TubRow) longitudinally along trunk; 6–9 tubercle rows transversely between hindlimbs (TubHip). Enlarged tubercles on crus and femur present in all individuals. Tail with small uniform scales dorsally and laterally, ventrally with uniform, small keeled scales (Subcaud = 0). One or 2 cloacal spurs on each side. Precloacal pores almost always present in males (7, 0–10), females usually lack pores (0, 0–6). Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Forefoot with narrow digits, 11–15 lamellae beneath fourth digit (4FingLm), 4–6 scale rows on palm; hindfoot with narrow digits, 17, 16–19 lamellae beneath fourth toe (4ToeLm).

Nactus inundatus, new species

Fly River Slender-toed Gecko

HOLOTYPE. USNM 325059, adult male from Papua New Guinea, Western Province, Emeti [-7.8547° 143.2451°], collected by Fred Parker on 1 November 1971 (Figure 34).

PARATYPES. Adult males, USNM 195757, 325063, and adult females, USNM 325061–062, 325066, with same collecting data as holotype.

DEFINITION. A bisexual taxon of geckos (Gekkoniinae) with moderate adults (♀♀ 48–58 mm, ♂♂ 45–54 mm SVL) with keeled subcaudals, postmental scales usually absent (0–8, median 0), moderate number of dorsal tubercle rows (11–15) and usually numerous tubercles (29–40, usually ≥ 32) in parasagittal row (TubRow), no tubercles present on dorsal surface of thigh and crus, and precloacal pores in males (13, 9–15), females usually with pores (4, 0–13) but fewer than in males. Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 52.0 mm SVL, 22.8 mm TrunkL, 20.2 mm SnForel, 13.7 mm HeadL, 9.1 mm HeadW, 6.3 mm HeadH, 3.8 mm EyeD, 3.8 mm NarEye, 3.7 mm Interorb, 1.7 mm SnW. Body proportions: 44% TrunkL/SVL, 38% SnForel/SVL, 26% HeadL/SVL, 17% HeadW/SVL, 66% HeadW/HeadL, 7% EyeD/SVL, 28% EyeD/HeadL, 28% NarEye/HeadL, 29% Interorb/HeadL, 12% SnW/HeadL.

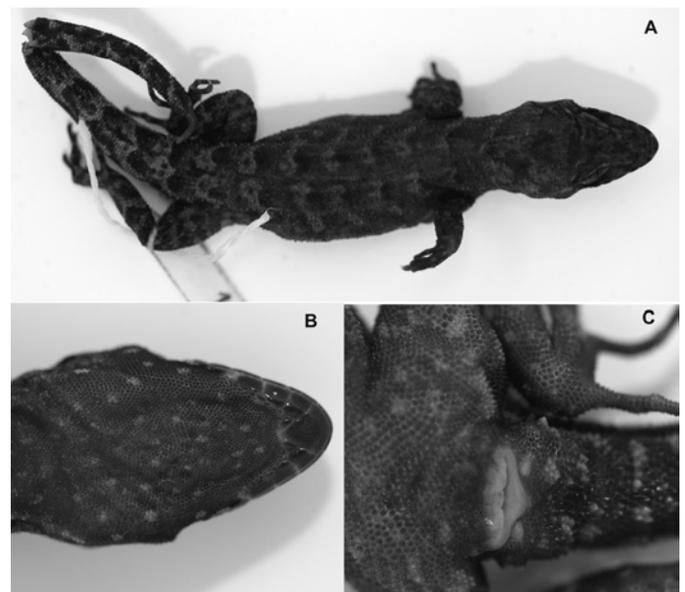


FIGURE 34. Holotype of *Nactus inundatus* (USNM 325059). (A) Dorsal view of entire body, (B) ventral view of head, and (C) ventral view of pelvis and thigh. (Photographs by E. Langan, USNM.)

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 strongly depressed on its mid-posterior half; 4 large supralabials (right) and 4 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly 3 granular loreal scales (right, 3 left), upper largest. Supranasals moderate sized, rounded posteriorly, anteriorly separated on midline by moderately enlarged granular scales and posteriorly bordered by granular scales. Scales on outer edge of eyelid slightly enlarged, forming low crenate border. Chin with large, pentagonal mental and no postmentals (Postm = 0). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach ventrolaterally to near edge of venter, 15 entire rows (DorsTub), and to mid-laterally on neck; 32 tubercles per row (TubRow); 9 rows transversely between hindlimbs (TubHip). Hindlimbs lack enlarged tubercles on upper and lower limbs (TubHindl = 0). Tail anteriorly with tubercle rows dorsally, laterally, and slightly overlapping onto ventral surface. Tail largely regenerated and ventrally with uniform small keeled scales (Subcaud = 0). Pair of cloacal spurs (CloacS) on right and left; distal edge rounded (CSTip = 0). Ventral scales from chin to vent small, granular to tuberculate. Precloacal pores 11. Forefoot with narrow digits, their lengths $3 \approx 4 > 2 \approx 5 > 1$; 16 lamellae beneath fourth digit (4FingLm), 7 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, their lengths $3 \approx 4 > 5 > 2 > 1$; 19 lamellae beneath fourth digit (4ToeLm); lamellae of first digit extend onto sole of foot to its heel as row of greatly enlarged scales.

Coloration in life not reported. In alcohol, background medium brown dorsally and laterally. Dorsally head with white to cream spots on top of snout and lores, fewer and less distinct on crown; small and irregular-shaped dark-brown postorbital stripe border above by white; supra- and infralabials medium brown with cream edges anteriorly and posteriorly at sutures, giving broad barred appearance, infralabials dark brown with cream to white sutures. Dorsally, neck and trunk to base of tail with dark-brown, ill-defined transverse bars with lighter-brown interspaces; distinct dark-brown transverse bar at base of tail with posterior cream border. Forelimb mottled medium brown and tan; hindlimbs with mottled brown dorsally and posteriorly with horizontal white bar border above by dark brown. Venter from chin to vent uniform light brown.

ETYMOLOGY. The specific name derives the Latin *inundatus* in reference to the origin of the species' landscape development from repeated flooding by the region's rivers, especially the Fly River.

VARIATION. Females and males display nearly identical metrics (adult ♀♀ 50.9, 48.0–58.1 mm; adult ♂♂ 50.7, 44.9–53.9 mm SVL) and share similar proportions (total adult sample): TrunkL/SVL 42.0%, 36%–47%; HeadL/SVL 26.9%, 25%–28%; HeadW/SVL 18.0%, 16%–20%; HeadW/HeadL 67.0%, 63%–72%; EyeD/SVL 6.9%, 6%–8%; EyeD/HeadL

25.7%, 23%–30%; NarEye/HeadL 30.8%, 26%–34%; Interorb/HeadL 27.0%, 23%–31%; SnW/HeadL 14.8%, 12%–17%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Snout with large rostral scale with middorsal depression and cleft posteriorly; supranasals moderate sized, usually in contact on midline or separated by small granular scale (internasal); large supralabials (3, 3–4) and infralabials (3, 3–4) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and usually (~85%) lacks postmentals (Postm = 0, 0–8); dorsally, trunk with 13, 11–15 (DorsTub) enlarged tubercles transversely on dorsum and with 36, 29–40 tubercles (TubRow) longitudinally along trunk; 8, 7–10 tubercle rows transversely between hindlimbs (TubHip). No enlarged tubercles on crus and femur (TubHindl = 0). Tail with small uniform scales dorsally and laterally, ventrally with uniform, small keeled scales (Subcaud = 0). Usually, pair of cloacal spurs (2, 1–2 CloacS) on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Precloacal pores, males 9–15, females usually with pores 0–13. Forefoot with narrow digits, their lengths usually $3 \approx 4 > 2 \approx 5 > 1$; 16, 13–18 lamellae beneath fourth digit (4FingLm), 6, 5–7 scale rows on palm; hindfoot with narrow digits, their lengths $4 > 3 > 5 > 2 > 1$ or $3 \approx 4 > 2 \approx 5 > 1$; 26, 18–22 lamellae beneath fourth toe (4ToeLm).

Coloration in life not reported. In alcohol, color and pattern match the general description of the holotype. The dorsal trunk pattern of transverse bars varies from faded to dark; in some dark bars divided at dorsal midline, from 5 to 6 bars between shoulders to sacrum. Forelimbs typically mottled dark and medium brown; hindlimbs (thigh) varying from mottled to horizontal light bar posteriorly; venter uniform light brown.

DISTRIBUTION. Principally, the flood plain of the Fly River north to Lake Murray and likely westward into Papua Indonesia (samples 64, 65, 66).

Highlands populations: Crater Lake, Chimbu Province (sample 62), and Waro, Southern Highland Province (sample 63)

COMMENTS. I have a sample of three adult females and an immature individual from Chimbu Province and an adult male and adult female from Southern Highlands. The former derives from the headwaters of the Purari River, and the latter derives from the headwaters of the Kikori River. Both of these rivers harbor the species *N. papua* in their lower reaches; thus, I consider both samples to represent *N. papua*.

VARIATION. The Chimbu females with a mean of 57.6 mm and range of 52.5–61.5 mm SVL match the average size range of the downstream *N. papua* sample and similarly share the other characteristics of the latter sample. Their postmentals are smaller (6–7 Postm) than the average for *N. papua* but only slightly so. They have no enlarged tubercles on their hindlimbs, a variable trait in *N. papua*. All other traits similarly match *N. papua*.

The same trait matching occurs for the two Southern Highlands adults. Both are 56 mm SVL, have modest-sized

postmentals (12, 16), have no enlarged tubercles of hindlimbs, and match *N. papua* in other traits.

Southern Papua Indonesia populations: Sabang (sample 67) and Wamena (sample 68)

COMMENTS. I have two samples of one adult individual each from two adjacent river drainages of south central Papua Indonesia: Lorenz River (male from Sabang) and Baliem River (female from Wamena). Because they are not strikingly different, I propose that they are western representatives of *N. undulatus*. The presence of a high number of precloacal pores (11) in each and a low number of forelimb lamellae (15) indicates that they are not representatives of the north coast *N. septentrionalis*.

DESCRIPTION. Female (Sebang) and male (Wamena) are similar in size (adult ♂ 49.2 mm; adult ♀ 51.9 mm SVL) and share similar proportions (total adult sample): TrunkL/SVL 37%–39%; HeadL/SVL 26%–27%; HeadW/SVL 17%–19%; HeadW/HeadL 66%–69%; EyeD/SVL 6%–8%; EyeD/HeadL 23%–25%; NarEye/HeadL 31%–36%; Interorb/HeadL 25%–27%; SnW/HeadL 15%–16%.

Typical head scale pattern of small, granular scales except for those bordering nares and mouth. Large supralabials (3) and infralabials (3) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Chin with large trapezoidal mental and small postmental (Postm = 4 in Wamena) and no genial scale between postmental and first supralabial; dorsally, trunk with 12–16 (DorsTub) enlarged tubercles transversely on dorsum and with 37–39 tubercles (TubRow) longitudinally along trunk; 8 tubercle rows transversely between hindlimbs (TubHip). No enlarged tubercles on crus and femur. Tail with small uniform scales dorsally and laterally, ventrally typically with uniform, small keeled scales (Subcaud = 0). Two cloacal spurs on each side. Ventral scales from chin to vent small, granular, somewhat larger on chest and abdomen. Forefoot with narrow digits, 15 lamellae beneath fourth digit (4FingLm), 7–9 scale rows on palm; hindfoot with narrow digits, 20–22 lamellae beneath fourth toe (4ToeLm).

Coloration not recorded.

Nactus undulatus (Kopstein, 1926)

Kei Slender-toed Gecko

Gymnodactylus pelagicus undulatus Kopstein, 1926:74 [type locality, “Elat, Gross-Kei”].

HOLOTYPE. RMNH 5095, adult male from Kei Islands Maluku Province, “Elat, Gross-Kei” [–5.6562° 132.9901°], collected by F. Kopstein on March 1923 (Figure 35).

DEFINITION. A bisexual taxon of geckos (Gekkoniinae), known from a single small adult male of 37.4 mm SVL, with smooth subcaudals, no postmental scales, low number of dorsal tubercle rows (12) and high number of tubercles (40) in parasagittal row (TubRow), no tubercles present on dorsal



FIGURE 35. Holotype of *Nactus undulatus* (RMNH 5095). Dorsolateral view of entire body. (Photograph by G. Zug.)

surface of thigh and crus, and moderate number of precloacal pores (10) in male. Diagnostic summary in Table 8.

DESCRIPTION OF HOLOTYPE. An adult male, 37.4 mm SVL, 15.2 mm TrunkL, 17.3 mm SnForel, 11.3 mm HeadL, 7.3 mm HeadW, 5.7 mm HeadH, 2.8 mm EyeD, 3.38 mm NarEye, 3.1 mm Interorb, 1.3 mm SnW. Body proportions: 40% TrunkL/SVL, 46% SnForel/SVL, 30% HeadL/SVL, 20% HeadW/SVL, 65% HeadW/HeadL, 8% EyeD/SVL, 25% EyeD/HeadL, 29% NarEye/HeadL, 27% Interorb/HeadL, 12% SnW/HeadL.

Head scales small and granular except for enlarged scales bordering nares and mouth. Large horizontal trapezoidal rostral scale; 5 large supralabials (right) and 5 infralabials (right) in front of anterior edge of orbit, first supra- and infralabial largest of respective series. Nasal scale contacts first supralabial, rostral, supranasal scales and posteriorly by granular loreal scales. Supranasals moderate sized and posteriorly bordered by granular scales. Chin with large, pentagonal mental and lacking postmentals (Postm = 0). Dorsum of neck and trunk with numerous rows of enlarged tubercles from nape onto tail; on trunk rows reach to middle of sides of trunk, 12 entire rows (DorsTub), and to mid-laterally on neck; 40 tubercles per row (TubRow); 8 rows transversely between hindlimbs (TubHip). Hindlimb with no tubercles on upper and lower limbs (TubHindl = 0). Tail anteriorly with tubercle rows dorsally, laterally, and slightly overlapping onto ventral surface. Tail ventrally with uniform small smooth scales (Subcaud = 1). Pair of cloacal spurs (CloacS) on right and left; distal edge irregular (CSTip = 1). Ventral scales from chin to vent small, granular to tuberculate. Precloacal pores 10. Forefoot with narrow digits; 13 lamellae beneath fourth digit (4FingLm), 6 scale rows between lamellae at base of first and fifth fingers (Palm). Hindfoot with narrow digits, and 17 lamellae beneath fourth digit (4ToeLm).

Coloration in life, “on the dorsum, short dark wavy cross-bands, interrupted on the midline; each truncated on the rear

edge by a small yellow line: on nape, an even brighter, somewhat V-shaped mark” (translated from original description in Kopstein, 1926:74). Coloration in alcohol not recorded.

ETYMOLOGY. The specific name derives from Late Latin *undulatus* for “wavy.” Choice presumably results from Kopstein’s impression of the dorsal markings.

DISTRIBUTION. Presently known from a single specimen from Kei Besar (Nuhu Yuut) in the Kei Islands (sample 69). A recent thorough survey of the Kei Islands (Karin et al., 2018) did not find this species.

A diagnostic summary of the New Guinean *pelagicus* complex is available in Table 8.

DIVERSITY AND DISTRIBUTION PATTERNS IN THE NEW GUINEAN HERPETOFAUNA

The number of New Guinean *Nactus* species (26) that my and Kraus’s (2005) data and analyses proposes is considerably greater than anticipated when Brad Moon and I initiated our study of Pacific *Nactus* in the late 1980s. Have I been overly zealous in recognizing differentiation among the populations (samples) of the larger *Nactus*? Future studies of genomic variation in and among the proposed New Guinean species will answer that question.

There is a tendency in recent descriptions of New Guinea herpetofauna to conclude with a comparison and an attribution to geological events (e.g., Kraus, 2013; Oliver et al., 2018). I do not believe that my morphological analysis and the interpretation thereof matches the detailed analyses provided by those cited articles; hence, I have decided to offer a different comparison. I offer a comparison of the distributions of other New Guinea amphibians and reptiles and show which ones match those of the proposed species of *Nactus*.

New Guinea *Nactus* are lowland forest species, commonly less than 300 m asl. Those individuals and samples from higher elevations (e.g., samples 10, 22, 50, 51, 54, 55, 59, 60, 62, 63, 67, 68) are from river valley floors amid mountains and continuous with lower-elevation populations (actually or likely). The species occurring in coastal areas derive largely from secondary forests or plantations of agricultural trees. Even *N. heteronotus* of the Central Province savanna occurs in small patches of scrub forest.

Nactus distributions can be segregated into four groups or patterns: transregional, broad regional, regional, and restricted. Of the species occurring in New Guinea and its associated islands, only the unisexual *N. pelagicus* is a transregional species. This species’ distribution is strictly insular and discontinuous, occurring on Bougainville and Manus. These two New Guinea populations are morphologically distinct from one another and the Pacific/Oceania populations. The distribution and morphology suggest waif dispersal (perhaps accidental introduction) and subsequent adaptation to the local environment, which appears to have resulted in minor, although detectible, morphological differentiation. Superficially, the larger (≥ 42 mm SVL) *Nactus*

species are look-alikes with the exception of *N. galgajuga* and *N. kuman*, both of which have bold, contrasting banded patterns on their trunks. The latter two have distinctly restricted distributions, with the former confined to the Black Mountains of northern Queensland and the latter to Manus Island of the Admiralty Group. The other restricted New Guinea species are largely insular species: *N. arfakianus* (Schouten Islands), *N. nanus* (northern PNG coast), *N. panaeati* (Panaeati Island), *N. fredkrausi* (Misima Island), *N. acutus* (Rossel Island), *N. amplus* (Sudest Island), and *N. undulatus* (Kei). The species with regional distributions are *N. rainerguentheri* (assuming most of Vogelkop), *N. grevifer* (Torricelli Mountains), *N. intrudusus* (Markham Valley), *N. kamiali* (NE PNG coast), *N. modicus* (Sudest and Rossel Islands), *N. sphaerodactylodes* (Sudest, Woodlark, and Rossel Islands), *N. chrisaustini* (Milne Bay mainland), *N. notios* (southern mountains, Milne Bay), *N. erugatus* (Owen Stanley terminus, Milne Bay), *N. heteronotus* (Central Province savanna), and *N. papua* (Kikori and Purari drainages). The broad regional species are *N. septentrionalis* (north coast Papua to Sepik River), *N. allenallisoni* and *N. aktites* (PNG north coast), *N. robertfisheri* (Bismarck Archipelago and Bougainville), *N. alotau* (PNG SE and S coast), *N. inundatus* (SW PNG and SE Papua), *N. vankampeni* (PNG north coast). Among all New Guinea *Nactus*, only *N. vankampeni* shows evidence of a species occurring on both the north and south coasts (see Heinicke et al., 2010: fig. 1), although I suspect that the south coast record is a misidentification. A south-north coast distribution is possible east of the Vogelkop neck in southern Indonesia Papua for *N. septentrionalis*. Presently, no *Nactus* samples are available from southwestern Indonesia Papua.

The lifestyle and the general requirement of moist environments might suggest that frog distributions would be unlikely to match any *Nactus*. Broadly, that supposition is true, although some anuran species’ distributions share geographic boundaries similar to those of *Nactus*. Presently, anurans, the only amphibians in New Guinea, are represented by six families: Ceratophryidae, Dicroglossidae, Hylidae, Microhylidae, Myobatrachidae, and Ranidae (modified from Allison, 1996: table 1; Menzies, 2006). The microhylids are the most diverse and speciose of these frog families with 16 genera and more than 300 species. There appears to be polyphyly in some of the microhylid genera, although the genera *Choerophryne* (~37 species), *Cophixalus* (~70 species), *Hylophorbus* (~12 species), and *Oreophryne* (~70 species) are likely monophyletic even though each appears to have deep lineage divergences within the larger clade (Köhler and Günther, 2008; also see Rivera et al., 2017). These latter four genera offer the potential of comparing distributional patterns for ones that are coincident with *Nactus* species. A difficulty, however, is that no one has yet mapped the species distribution patterns of all or most of the species in any of these genera across the entirety of New Guinea. The difficulty of finding matching distributions is compounded because many of the species are known from one or a few specimens and commonly only from the type locality.

Among the preceding genera there are some distributions similar to those of *Nactus* species, but most of the microhylid species are montane inhabitants, typically above 300 m. Some examples of matches or near matches are as follows: Kraus and Allison's (2001) map suggests a regional distribution for *Choerophryne proboscidea* similar to that of *N. allenallisoni*. A broad study of relationships within *Choerophryne* (Oliver et al., 2017) shows one clade with a composite distribution that largely matches the combined distribution of *Nactus septentrionalis* and *N. allenallisoni*, although the study does not provide distributions for the individual species in the clade. *Cophixalus balbus* is a Yapen Island resident like *N. arfakianus*; *Coph. verrucosus* and *Coph. riparius* overlap with several of the Milne Bay *Nactus* species, *Coph. cupricarenum* co-occurs on Rossel Island with *N. amplus* and *N. modicus*, and *Coph. variabilis* shares the geographic extent of Milne Bay to Central Province (Kraus, 2012) with *N. alotau*, except the former is montane versus coastal plain. Differentiation of *Asterophrys turpicola* populations on Yapen and the Wondiwoi Mountains adds support to the likelihood of speciation of *Nactus arfakianus* and *N. rainerguentheri*, two species recognized herein in small samples.

Pelodyradid frogs are the next most speciose anurans in New Guinea. Presently, they comprise two genera: *Litoria* with more than 70 species and *Nyctimystes* with more than 30 species. Even though both genera have their greatest diversity in montane habitats, there are species sharing similar distributions with *Nactus* species. *Nyctimystes cheesmanae* occurs in southeastern New Guinea and the D'Entrecasteaux Islands, *Ny. perimetri* occurs on Sudest and Rossel, and *Ny. avocalis* occurs on Goodenough Island. *Nyctimystes humeralis*, although a montane inhabitant, has a south coast distribution from Milne Bay to Central Province like *N. alotau*. *Litoria* and *Ranoidea* have more lowland species, a few with distributions shared with or similar to those of *Nactus* species. *Ranoidea auae* is a Papuan lowland species from the Purari River through the Fly lowlands and on adjacent islands; *L. rubella* ranges across the Trans-Fly region and northern Australia, with a similar distribution occurring for one of the numerous morphs of *L. bicolor*. *Litoria bibonius* appears on Goodenough and Normanby Islands; *L. flavescens* occurs only on Normanby Island, and *R. impura* ranges from Central Province to Milne Bay. Aside from *R. caerulea* and *L. infrafrenata*, two species readily transported by humans, few lowland *Litoria* and *Ranoidea* species occur on both the north and south coasts.

In contrast to the microhylids and hylids, the myobatrachids have the fewest species in New Guinea even though they are represented by four genera (Menziez, 2006): *Crinia*, *Lechriodus*, *Limnodynastes*, and *Mixophyes*. Only the first two genera have species with broad enough distributions for comparison. The single New Guinea *Crinia* species, *Crinia remota*, occurs in the Trans-Fly lowlands, and this distribution matches that of *N. inundatus*. *Lechriodus* has three New Guinea species and a far-removed species in northeastern New South Wales, Australia (Zweifel, 1972). This latter disjunct species occurs well south of the Australian *Nactus* species. The distributions of the three New

Guinea *Lechriodus* (Zweifel, 1972: fig. 2 map) shows that none of the species match any *Nactus* species. *Lechriodus aganoposis* is a montane species of the Huon Peninsula and Central Cordillera. *Lechriodus melanopyga* has a broad regional distribution in the lowlands of the north and south coasts of the main New Guinea island, and *Lechriodus platyceps* is largely a Vogelkop species.

Until 2006, ranid frogs included a diverse assortment of species and a single family in New Guinea. A phylogenetic classification resulted in New Guinea ranids becoming three families (Ceratobatrachidae, Dicroglossidae, Ranidae). The New Guinea ceratobatrachids contains a single genus, *Cornufer*, whose species extend eastward from the Moluccas Islands to Fiji. There are approximately 20 species in New Guinea, the Bismarcks, and Bougainville, and none of the species occur broadly on the south coast. Only *Cornufer papuensis*, a transregional species (Moluccas eastward to Bougainville, D'Entrecasteaux, and mainland Milne Bay) edges into southern Papua Indonesia. The remaining species are largely restricted to single, isolated mountain ranges on the mainland, with numerous species also of restricted ranges in the Admiralty and Bismarck Archipelagos, particularly numerous in New Britain.

The New Guinean dicroglossids consist of *Fejervarya* and *Limnonectes* with supposedly four species in New Guinea, although *Limnonectes grunniens* appears to be the only truly New Guinean taxon. It is a bicoastal species occurring in the lower reaches of the larger rivers on the north and south coasts from the Sepik to the Fly River (Menziez, 2006) and having an overlapping distribution on the north coast with *N. septentrionalis* and possibly on the south coast with *N. inundatus*.

The remaining ranids are in the family Ranidae and, in New Guinea, are contained in a single genus, *Papurana*, presently with about a dozen species. Most species appear to have regional distributions on mainland New Guinea (Kraus and Allison, 2007; Frost, 2019: AWS6.0) with *P. daemeli* also occurring on Cape York and New Britain. Although some species have widespread or broad regional and seemingly continuous distributions, for example, *P. garritor* and *P. papua*, other species (*P. supragrisea*, *P. arfaki*) might also be broadly distributed, but the taxonomic status of the various populations throughout the broader range is uncertain (Kraus and Allison, 2007; Donnellan et al., 2010). Two distributional aspects of several taxa are of interest: presence on both the north and south coasts for lowland-occurring species (e.g., *P. daemeli*, *P. garritor*, *P. papua*) and the occurrence of mainland species on Goodenough, Ferguson, and Trobriand Islands (*P. milneana*, *P. waliesia*). Both patterns contrast sharply with those of *Nactus* species.

Among the reptiles, the "land-based" species of turtles and crocodylians are aquatic species and largely, if not exclusively, with either a south or north coast distribution. The north and south coast populations of the freshwater crocodile (*Crocodylus novaeguineae*) have long been recognized as distinct species, although the south coast one has only recently received formal recognition (*Crocodylus halli*). Of the three genera of chelids

(Rhodin et al., 2017), only one species, *Eelseya schultzei*, occurs on the north coast and widely from Vogelkop neck to the Northern Province. Most other chelids are concentrated in the Trans-Fly area and westward into southern Indonesia Papua. The exception is *Emydura subglobosa*, occurring from the Vogelkop neck to the Central Province. The only freshwater cryptodiran turtle is *Carettochelys*, a Trans-Fly species shared with northern Australia.

New Guinean lizards consist of six families: Agamidae, Dibamidae, Gekkonidae, Pygopodidae, Scincidae, and Varanidae. Focusing on four genera in three families offers an oversight of the diversity of distribution patterns in New Guinean lizards. The agamid *Hypsilurus* has nearly 20 species (Manthey and Denzer, 2016; Uetz et al., 2019), about a third of which have restricted distributions that are either restricted to the type locality (e.g., *Hy. binotatus*, *Hy. geelvinkianus*) or are uncertain (e.g., *Hy. nigrigularis*, *Hy. tenuicephalus*). Broad regional taxa include *Hy. auritus*, *Hy. godeffroyi*, and *Hy. magnus*, matching distributions of *N. septentrionalis*, *N. robertfisheri*, and *N. septentrionalis*, respectively. *Hypsilurus modestus* occurs broadly on mainland New Guinea and associated islands, including Kei, Aru, and the Admiralty-Bismarck Archipelago, but surprisingly not in the Louisiade Archipelago. *Hypsilurus papuensis* is a complex of undescribed species, and once studied, the nominal species is likely to have a Central Province distribution similar to that of *N. heteronotus*.

Dibamus novaeguineae is a widespread Sunda species and occurs only marginally in western Papua Indonesia. New Guinean geckos include six genera, including *Nactus*. *Cyrtodactylus* is the most diverse gecko group, with more than 25 species, many with distributions known only from their type localities. Some of the latter are Louisiade Archipelago species (Kraus, 2008), for example, *C. louisiadensis* (Misima, Sudest), *C. klugei* (Sudest), *C. murua* (Woodlark), *C. robustus* (Rossel), and *C. tripartitus* (Misima). These distributions largely match the *Nactus* species occurring in this archipelago, although the *Nactus* species occur on more islands and are mainly allopatric, except *N. amplus* and *N. modicus*, both occurring on Sudest and Rossel Islands. Several *Cyrtodactylus* have north coast distributions similar to those of *N. septentrionalis*, for example, *C. boreoclivus*, *C. equestris*, *C. mimikanus*, and *C. novaeguinea*, and *N. allenallisoni*, for example, *C. rex* and *C. seromowaiensis*. On the south coast, *C. lorae* matches *N. papua*. The shared habitus of these two genera would suggest competition, but species of *Cyrtodactylus* usually are larger and arboreal in contrast to more terrestrial *Nactus*.

Gekko vittatus and *Gekko monarchus* are the only *Gekko* species in New Guinea, and both have transregional distributions, from the north coast of PNG into the Solomon Islands for the former and from the north coast into the Malaya Peninsula for the latter. Similarly, *Gebyra* has 11 species in New Guinea, and most New Guinea-occurring species are transregional ones. *Gebyra dubia* occurs in eastern Australia and the Torres Strait Islands into south central New Guinea. *Gebyra baliola* also occupies the strait islands into southern New Guinea, sharing a

common distribution with *N. papua* and *N. inundatus*. *Gebyra mutilata* and *Gebyra oceanica* extend eastward into Oceania like *N. pelagicus*. *Gebyra papuana* appears to have a distribution overlapping *N. septentrionalis*, *N. allenallisoni*, and perhaps *N. aktites*. *Gebyra rohan* occurs on the two large islands of the Admiralties and Mussau. Is its presence on Mussau a World War II import? Otherwise, *G. rohan* matches the distribution of *N. kunan*.

Nine species of *Lepidodactylus* are presently reported for New Guinea. The commensal *Lep. lugubris* is a transregional occurring widely in Sundas and into Oceania. *Lepidodactylus guppyi* and *Lep. woodfordi* are also transregional, the former from New Britain into the Solomons and the latter from the Fly River area to Cape York Peninsula. Of the strictly New Guinean species, *Lep. browni* and *Lep. orientalis* are Central Province inhabitants like *N. heteronotus*; *Lep. magnus* is a central highland species, and *Lep. pulcher*, like *N. kunan*, occurs only in the Admiralties.

Only two species of Pygopodidae occur in New Guinea; neither matches the distribution of any *Nactus*. *Lialis jicari* is widespread in the New Guinea lowlands, both the north and south coasts. *Lialis burtoni* occurs widely in Australia and, peculiarly, only in the Central Province.

The Scincidae are the most diverse (15 genera) and speciose (130 + species) lizards of New Guinea. I examine only three of the genera here, the only ones with wide generic analyses (*Carlia* [Zug, 2004], *Cryptoblepharus* [Horner, 2007], *Emoia* [Brown, 1991]). *Sphenomorphus* is excluded because it is a polyphyletic aggregation of species. The distributions of several *Nactus* species nearly match those of *Carlia*, but only *Ca. luctuosa* of the Central Province and *N. heteronotus* are nearly identical. Other *Carlia* species overlap in part or include several *Nactus* species distributions. *Carlia fusca* and *Ca. pullum* encompass *N. septentrionalis*; *Ca. mysi* occurs with *N. allenallisoni*, *N. aktites*, *N. robertfisheri*, *N. intrudusus*, and *N. kamiali*. The Milne Bay *Nactus* are sympatric with *Ca. eothen*. *Nactus papua* and *Ca. aenigma* have matching distributions, and *N. inundatus* and *Ca. aramia* largely overlap in occurrence. Both *Ca. beccarii* and *N. undulatus* occur in the Kei islands.

Outside of Australia, *Cryptoblepharus* is predominantly a coastal species (Horner, 2007). One species, *Cr. richardsi* (Misima), occurs in the Louisiade Archipelago, matching the distribution of *N. fredkrausi*. Another insular match is *Cr. keiensis* and *N. undulatus* in the Kei Islands. *Cryptoblepharus yulensis* is a Central Province species like *N. heteronotus*.

Emoia is the most speciose lizard genus in New Guinea, with nearly 40 species on mainland New Guinea, the Admiralties, the Bismarcks, and the eastern island groups of Milne Bay Province (Brown, 1991). Using Brown's (1991) and Mys's (1988) distributional data, New Guinea *Emoia* match the four distributional patterns delimited for bisexual *Nactus* species. Only a few *Emoia* species match closely the distribution of a *Nactus* species: for example, *E. brongersmai*, *E. digul*, and *E. tropidolepis* in the Fly River and Digul River drainages with *N. inundatus*; *E. physicae*

purari in the Purari drainage with *N. papua*, although apparently they do not co-occur in the Kikori basin; and *E. battersbyi* and *E. loveridgei* broadly on the north coast with *N. septentrionalis* but extending farther eastward on the coast. Additionally, there are other *Emoia* species (e.g., *loveridgei*, *popei*, *tetrataenia*) that have PNG north coast distributions overlapping those of *N. allenallisoni* and *N. aktites*, although they extend farther eastward into or beyond the lowlands of the Huon Gulf. *Emoia bismarkensis* matches the distribution of *N. robertfisheri*, although not including Bougainville. *Emoia submetallica* occurs on both the north and south coasts of central Papua New Guinea, a north and south coast pattern not seen in any *Nactus*. It seems likely that the herpetofaunas of the outer Milne Bay islands are largely endemic. Although the *Emoia* do not divide into as many insular species as I have recognized, Brown (1991) recognized unique populations in the Rossel, Fergusson, and Louisiade groups. *Emoia mivarti* is an Admiralties endemic, and *E. kitchneri* is a Kei one. A number of *Emoia* (*atrocostata*, *caeruleocauda*, *jakati*) rival *Nactus pelagicus* in its broad Pacific Islands distribution.

Of the 13 *Varanus* species reported, only 11 appear to have reliable New Guinea occurrence. Several (*V. gouldi*, *V. panoples*, *V. similis*) are Australian species with south New Guinea populations, and *V. spinulosus* is a Solomon Islands species occurring on Bougainville. *Varanus indicus*, a transregional species, is a widespread coastal species from the Lesser Sundas to Micronesia, although its type locality is NW New Guinea; its eastern occurrence somewhat matches that of *N. pelagicus*. Some of its former subspecies, *V. doreanus* and *V. douarrha*, are single-island species, New Britain and New Ireland, respectively, and are encompassed in the distribution of *N. robertfisheri*, as is the Mussau *V. semotus*. *Varanus prasinus* occurs island-wide in the lowlands, and *V. salvador* occurs on the southern coast from the Vogelkop to the PNG Gulf Province.

Of the seven families of New Guinean snakes, the Boidae (Candoiidae), Pythonidae, Colubridae, and Elapidae have genera of terrestrial and semiaquatic snakes with sufficiently well-known distributions for comparison with *Nactus* distributions. The boid *Candoia* has three species, *Candoia aspersa*, *Candoia carinata*, and *Candoia paulsoni* (Reynolds and Henderson, 2018) in New Guinea. Their north coast New Guinea distributions are largely sympatric with and overlap those of *N. septentrionalis* and, westward, *N. kamiali*, and their distribution in the Bismarcks overlaps *N. robertfisheri*. *Candoia paulsoni* has a more easterly distribution and has several subspecies, three of which have complementary distributions with *Nactus* species. *Candoia paulsoni mcdowellii* has a PNG south coast distribution similar to that of *N. alotau*, *Candoia paulsoni rosadoi* is endemic to Misima like *N. fredkrausi*, and *Candoia paulsoni sadlieri* is endemic to Woodlark Island. The pythonids are a somewhat more diverse group in New Guinea than the boids, and their distributional similarities often center on the south coast and mainly in the Trans-Fly area. *Bothrochilus* has several species in New Guinea, *B. albertisii*, *B. fredparkeri*, *B. huonensis*, *B. meridionalis*, *B. montanus*, and perhaps a few more (Schleip, 2008, 2014), but their

systematics is muddled, so it is difficult to compare distributions, although if *B. huonensis* and *B. montanus* are valid taxa, their distributions match *N. intrudus* and *N. kamiali*, respectively. *Bothrochilus boa* is restricted to the Bismarcks, as is *N. robertfisheri*. *Liasis papuanus* and *Morelia viridis* are widespread in New Guinea, and the latter appears to be genetically differentiated on either side of the central mountain range (Rawlings and Donnellan, 2003). Of the remaining two New Guinean pythons, *Simalia amethystina* has an island-wide distribution and occurs also in Australia and the Moluccas. *Simalia boeleni* is restricted to central mountain range and appears to be genetically uniform throughout its distribution (Austin et al., 2011).

Five genera of colubrid snakes occur in New Guinea. Two (*Lycodon capucinus*, *Boiga irregularis*) are represented each by a single species; however, the genetics of *Boiga* (Richmond et al., 2014) shows differentiation patterns similar to those found in the speciation of *Nactus* as proposed here. The former occurs only marginally in westernmost New Guinea, and the latter is a widespread lowland snake on both coasts and in tropical Australia. The remaining three genera are moderately speciose (O'Shea, 1996; Uetz et al., 2019): *Dendrelaphis* has seven species, *Stegonotus* has eight species, and *Tropidonophis* has 14 species. Of the *Dendrelaphis* species, *D. calligaster* is a transregional species occurring from the Lesser Sundas to Solomon Island and northern Australia. *Dendrelaphis punctulatus* is also transregional, widespread in New Guinea and northern Australia. Of the remaining taxa, *D. gastrostictus* has a patchy distribution, the Huon Peninsula, Fergusson and Normanby Islands, then south central PNG and the trans-Fly region; *D. lineolatus* is similarly bicoastal and also in the Bismarck and Louisiade Archipelagos. *Dendrelaphis macrops* has a peculiar bicoastal distribution that is likely erroneous. A revised taxonomy of *Stegonotus* (Kaiser et al., 2018, 2019; Ruane et al., 2018) suggests there are no New Guinea island-wide species, with most having regional or restricted regional distributions. *Stegonotus admiraltiensis* occurs on Manus, *S. diehli* and *S. poecki* occur in Madang Province, *S. parva* occurs on Yapen, and *S. keyensis* occurs in the Kei Islands. Two species, *S. guentheri* and *S. reticulatus*, have broader distributions, Fergusson, Goodenough, Normandy, and Trobriand Islands for the former and the southern slope of the mountains from Milne Bay to Central Province for the latter. The former overlaps with several species of *Nactus*, and the latter is similar to *N. alotau*. *Tropidonophis* is presently the most speciose (more than 14 species) colubrid snake genus on New Guinea (Malnate and Underwood, 1988; O'Shea, 1996; Uetz et al., 2019). *Tropidonophis multiscutellatus* and *Tropidonophis doriae* appear to occur broadly on the north and south coasts. *Tropidonophis mairii* is transregional in the Trans-Fly region and tropical Australia. *Tropidonophis hypomelas* is a Bismarck species (Kraus and Allison, 2004), similar in distribution to *N. robertfisheri*.

The terrestrial elapids have eight or nine genera in New Guinea, and only two, *Aspidomorphus* and *Toxicocalamus*, have experienced broad speciation within New Guinea and adjacent

islands. *Aspidomorphus* has three species (Metzger et al., 2010), with *A. muelleri* throughout the lowlands of New Guinea, *A. schlegeli* from the Sepik westward throughout the Vogelkop, and *A. lineatocollis* from Madang eastward into the Louisiade Archipelago. *Toxicocalamus*, a predominantly montane snake, has 15 species (O'Shea et al., 2018), most of which have small ranges and are largely known from the vicinity of their type locality. Speciation has been high in the Louisiade Archipelago with species on Fergusson (*T. nigrescens*), Woodlark (*T. longissimus*), Misima (*T. misimae*), Sudest (*T. mintoni*), and Rossel (*T. holopelturus*). The latter pattern matches that of several *Nactus*.

The other genera of New Guinean elapids are principally lowland inhabitants. *Acanthophis* has two lineages in New Guinea (*laevis*, *rugosus*; Wüster et al., 2005; Shine et al., 2014). The latter species appears to be primarily a Trans-Fly species, and the former is a widespread species in Papua Indonesia and Papua New Guinea. *Micropechis ikabeka* is similarly widespread, both north and south of the Central Cordillera, although it is seemingly absent from the lowlands of the Trans-Fly area and westward into Papua. *Oxyuranus scutellatus* and *Pseudechis papuanus* appear to be widespread south coast/lowland species. The distribution of the two *Pseudechis* are inadequately documented. None of the preceding four genera have distributions matching any *Nactus* species.

The preceding attempt to show matches and mismatches of the distribution of other New Guinean anurans and reptiles with those of the newly recognized species of the *Nactus pelagicus* complex suffers from an inadequacy of well-delimited distributions for most species. (I note my dismay that the Bishop Museum's Papuan Herpetofauna website is no longer available as of April–May 2019. The disappearance of such web resources is not an uncommon phenomenon and a strong argument for publication of hardcopy and their deposition in libraries.) In spite of the limitation of distributional data on the New Guinea herpetofauna and my selective interpretation of it, a number of distribution commonalities are identified. Foremost is the low frequency among the lowland anurans and reptiles of widespread species and of bicoastal species, certainly a phenomenon for *Nactus*. *Nactus* has no bicoastal species. Bicoastal distributions are not rare, although they are not a common distribution feature of the New Guinea herpetofauna. Among the lowland taxa, this pattern appears more frequently in the larger-bodied ones, for example, *Nyctimystes infrafronatus*, *Papuarana*, *Varanus prasinus*, and *Boiga irregularis*.

A lowland distribution from the neck of the Vogelkop to the Sepik-Ramu area is shared by a variety of frogs, lizards, and the single north coast chelid turtle. Although the distributional data are not precise, neither the western nor the eastern limits of the ranges match among the taxa. In the east, some end before reaching this area, and others extend to the Huon Peninsula. No genus with the possible exception of *Emoia* shows the overlapping distributions of species in the Sepik to Huon corridor observed in *Nactus*. Kraus and Myers (2012) noted that many species with restricted ranges on the north coast, particularly those in

the lowlands of the Torricelli Mountains area, likely have more extensive distributions and recently described species from the far western (i.e., Papua Indonesia) north coast likely have broader ranges extending to the Huon Peninsula. Perhaps that is so, but the complex and overlapping distributions of the *Nactus* species from the Sepik River to the base of the Papuan Peninsula suggest otherwise (see comments below). Similarly, I have found no other herpetofauna species with a Markham Valley distribution like that of *N. intrudusus* or a north coast Peninsular Papua distribution like that of *N. kamiali*. Milne Bay and the Louisiade Islands have been a speciation center for *Nactus* and an assortment of other New Guinea frogs and reptiles (enumerated earlier in this distributional section). Insular speciation is a common phenomenon. The complex geological history (Baldwin et al., 2012) indicates that each island group (exclusive of the Fergusson Islands) arose from discrete tectonic events and have always been separated by deepwater channels, thereby suggesting dispersal and subsequent differentiation rather than a vicariance origin. The speciation patterns along the southern or gulf coast of New Guinea is less clear except for the Central Province savanna and the Trans-Fly shared species or closely related pairs (e.g., Heinsohn and Hope, 2006; Wüster et al., 2005) in which populations appear to have dispersed from Australia and some of them differentiated and others did not; presumably, the latter are more recent dispersants.

In conclusion, this overly generalized comparison of herpetofaunal distributions demonstrates some similarities of *Nactus* species with other herpetofaunal species, especially in the Milne Bay portion of the Papuan Peninsula and the Louisiade Archipelago. A striking difference in *Nactus* diversity occurs along the northern PNG coast from the Sepik-Ramu deltas to the Huon Peninsula; only part of this area has moderately high species richness (Tallowin et al., 2017). I look forward to a more integrated analysis of New Guinea frog and reptile distributions, such as those presented by Allison (1996) and Allison and Leisz (2009).

ACKNOWLEDGMENTS

As I mentioned in the preface, this study had its genesis during my stay (September 1971 to February 1972) at the Papua New Guinean government's Wildlife Laboratory, Moitaka, although it formally became a data-collecting research project in 1989. Its long tenure has engendered a debt of gratitude to a diverse and large group of individuals and institutions to whom I offer most appreciative thanks.

Financial support derived almost exclusively from the Smithsonian and the National Museum of Natural History from 1970 through 2008. That support had a multitude of fund names over the years and was essential for the initial fieldwork in Papua New Guinea and, subsequently, for a multitude of museum collection visits. The collections hosting my visits were American Museum of Natural History; Australian Museum, Sydney; The Natural History Museum (formerly British Museum of Natural History);

Bernice P. Bishop Museum; Bean Life Science Museum, Brigham Young University; California Academy of Sciences; Field Museum of Natural History; Institut royal des Sciences naturelles de Belgique; Museum of Comparative Zoology, Harvard University; Louisiana Museum of Natural History, Louisiana State University; Museum für Naturkunde, Humboldt-Universität zu Berlin; Muséum National d'Histoire Naturelle, Paris; Naturhistorisches Museum Wien; Queensland Museum; Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie); South Australian Museum, University of Adelaide; Senckenberg Forschungsinstitut und Naturmuseum (formerly Natur-Museum und Forschungs-Institut Senckenberg); USNM—National Museum of Natural History, Smithsonian Institution; and Zoölogisch Museum, Universiteit van Amsterdam. Many of these collections

hosted multiple visits and most kindly lent specimens. I appreciate and thank the collections management staffs of all of them for their assistance and hospitality.

Personal help and encouragement were rendered by Allen Allison, Chris Austin, Robert Fisher, Fred Kraus, and Brad Moon. The first draft of the monograph manuscript was reviewed and improved by Robert Fisher, Aryeh Miller, and Robert Sprackland, to all of whom I offer a big thank-you for volunteering to read a large manuscript. As always, I appreciate Ken Tighe's efforts to ensure the correct citation of USNM numbers. I give special thanks to my wife, Patricia, who accompanied me on many museum visits, recorded specimen data, and input them into Excel files.

Appendix A: Character Definitions

SEX AND MATURITY. Examination of the gonads revealed sex and maturity. Females were considered mature when they possessed vitellogenic follicles, typically >1.5 mm diameter, oviducal eggs, or stretched oviducts; males were considered mature when the testes and epididymides were enlarged, supplemented by the presence of secreting precloacal pores.

COMMENTS ON CHARACTERS. Several researchers have attempted to quantify digit shape and length, as well as other traits. Although I support quantification because it allows statistical analysis and presumably removes a degree of bias or subjectivity, many voucher specimens are not carefully prepared, resulting in bent or folded specimens or parts thereof. Thus, quantification of some characters implies a degree of accuracy that does not exist. My selection of mensural characters (Table A1) emphasizes those possessing termini ending on bone and along axes that have rigorous bony struts, reducing compression or bending. SnForel and TrunkL, for example, are two useful measurements that, nevertheless, can have significant variation resulting from poor preparation.

TABLE A1. Abbreviations and definitions for characters examined.

Character class and abbreviation	Character name	Definition
Measurements		
EyeD	Eye diameter	Greatest horizontal distance across the exposed eyeball
HeadH	Head height	Distance from bottom of jaws to top of head at jaw articulation
HeadL	Head length	Distance from tip of snout to anterior border of ear opening
HeadW	Head width	Transverse distance at jaw articulation just anterior to ears
Interorb	Interorbital distance	Transverse distance between anterior edges of orbits
NarEye	Nares to orbit distance	Distance from anterior edge of orbit to naris
SnForel	Snout to forelimb distance	Distance from tip of snout to anterior edge of forelimb insertion
SnW	Snout width	Internarial distance from naris to naris
SVL	Snout-vent length	Distance from tip of snout to anterior edge of vent
TrunkL	Trunk or body length	Distance from axilla to groin
Scalation		
CloacS	Cloacal spurs	Number of enlarged and projecting scales in a cluster on one side of tail
CSTip	Cloacal spur's tip	0, spurs with blunt, rounded tips; 1, spurs with sharp, conical tips
DorsTub	Rows of dorsal tubercles	Number of tubercle rows at midbody
FemPor	Femoral pores	Number of femoral pores
ForefLm	Forefoot lamellae	Number of lamellae on fourth finger of forefoot
HindfLm	Hindfoot lamellae	Number of lamellae on fourth toe of hindfoot
Inflab	Infralabial scales	Number of entire infralabials from mental scale to anterior edge of orbit
Palm	Palm scales	Number of scales on palm between first enlarged lamella below first finger and first enlarged lamella below fifth finger
PmLab	Postmental-infralabial contact	Number of scale rows between first infralabial and postmental scales
PoreC	Femoral and precloacal pore rows in contact	0, not continuous; 1, continuous
Postm	Postmental scale size	Area of postmental scale estimated by number of chin scales occupying a similar-sized area as postmental; always recorded as an even integer
PreclPor	Precloacal pores	Number of open and secreting precloacal pores
Subcaud	Subcaudal scales	0, keeled; 1, smooth
Suplab	Supralabial scales	Number of entire supralabial scales from rostral scale to anterior edge of orbit
TubRow	Tubercles in a parasagittal tubercle row	Number of tubercles in second and/or third right parasagittal row from above axilla to above inguen
TubHip	Tubercle rows over hips	Number of tubercle rows dorsally across hips
TubHindl	Tubercle distribution on hindlimb	0, no tubercles on hindlimb; 1, tubercles only on crus; 2, tubercles above and below knee
TubDens	Tubercle density on thigh	Relative density of tubercle dorsally on the anterior half of the thigh: 0, none or widely scattered small tubercles; 1, a few widely spaced enlarged tubercles; 2, many large, nearly abutting tubercles on anterodorsal surface of thigh

Appendix B: Sample Numbers, Geographic Names, and Specimens Examined

Museum abbreviations follow Sabaj Pérez (2010); also see the Acknowledgments. The specimens are arranged numerically by locality; each locality is given a standard name. All localities were checked with Google Earth, and their geocoordinates were converted to decimal values.

1. Morotai [2.3218 128.4572], BYU 7331, 7540.
2. Numfoor Island (Japen Sea [=Teluk Cenderwasih/Cenderawasich Bay]) [-1.0411 134.8833], UMMZ 122449.
3. Biak Island (Japen Sea [=Teluk Cenderwasih/Cenderawasich Bay]) [-1.0270 135.9769], BPBM 3951.
4. Yeretuar (Vogelkop, neck) [-2.7592 134.5851], ZMB 62760.
5. Nabire to Mapai (Vogelkop, neck and trunk) [-3.6378 135.6772], BPBM 6156, ZMB 58589–590.
6. Toem [-2.0000 139.0167], MCZ R49264–268, USNM 119239–240.
7. Jayapura [-2.5328 140.7164], ZMA 15378.
8. Utai [-3.389 141.5847], BPBM 18954–956.
9. Aitape (vicinity of) [-3.1427 142.3500], RMNH 8831A–D.
10. Torricelli Mountains (Sandaun Province) [-3.4017 142.2499], BPBM 23360–362; Milom [-3.4880 142.0535], AMNH 100061–062; Nuku [-3.6751 142.4822], AMNH 100059–060; Kumnatei [-3.45 142.12], IRSNB 15802A–S; Lumi [-3.4740 142.8107], AMNH 100056–058; Maprik [-3.6296 143.0550], MCZ R153031.
11. Wewak: Wewak Catholic Station [-3.588 143.63], AMNH 105023–026, 105028–029, BPBM 23358.
12. Sepik River: Ambunti [-4.2138 142.8151], AMNH 99556–567; Kubka (=Kabuka) [-4.3111 142.3725], FMNH 14030.
13. Wagu [-4.3788 142.7273], BPBM 17323; Hunstein River [-4.4321 142. 7414], BPBM.AA 13621.
14. Northwest Madang Province, mountains: Mararup (=Mikarup) [-4.3167 144.7833], IRSNB 16524.1777, 16524.1787, 16524.1792, 16524.1795.
15. Northwest Madang Province, coast: Awar [-4.1363 144.8664], IRSNB 15875.1500, 15875.1512, 15875.1516, 15875.1526, 15875.1547, 15875.1569–70, 15875.1618, 15875.1621, 15875.1649; Bogia [-4.2754 144.9710], IRSNB 26.480A–B, 14438; Hatsfeldhafen (=Hatsfeldhaven) [-4.4078 145.1500], IRSNB 16519A–I.
16. Manam Island [-4.0813 145.0450], AMNH 104924–934; IRSNB 15867.1196, 151198–1200, 151206–1208, 151211; Boisa Island [-3.9956 144.9663], IRSNB/Mys 1191–92, 1212, 1216.

17. Karkar Island [-4.6371 145.9727], AMNH 104935-945, 104949, 104952; IRSNB 16837.33-34, 16837.36-37, 16837.39-40, 16834.4.
18. Alexishafen area: Baiteta village [-5.0054 145.7504], BPBM 05806, 24066-068, 24071, 31467, BPBM.JW 12, 18-19, 48, USNM 566875-876; Alexishafen [-5.0934 145.7971], AMNH 104873-877, AMS R31260-262, R31268, R31272-273, R31278, R31281, R31284, R31291-92, R31297, IRSNB 16456A-G; Siar Plantation [-5.1667 145.7500], AMS R124018-030, R124050, R124052-053.
19. Alexishafen area: Siar Plantation [-5.1667 145.7500], AMS R124051 [not duplicate; diff. sp].
20. Madang (vicinity of town) [-5.2239 145.8036], CAS 126710-711, 126713, 134376-378, MCZ R101533; Madrass Plantation [-5.1814 145.7711], MCZ R124293-295, R124302-304.
21. Bom [-5.4276 145.7320], IRSNB 15871.1373, 15871.1379, 15871.1384-85, 15871.1387, IRSNB 16526.1380, 16526.1383.
22. Finisterre Range [Madang Province]: Boana [-6.4323 146.8254], MCZ R98759.
23. Gusiko (=Gusika) [-6.4529 147.8464], AMNH 66668, USNM 119176, 119234-238.
24. Finschhafen [-6.5985 147.8533], USNM 159915-919.
25. Lae [-6.7333 146.9999], AMNH 95175-177, 103242-243, AMS R13255, SAM 03671; upper Markam, AMNH 92664.
26. Admiralty Islands (Manus) [-2.0958 146.9616], AMS R29071-074, 31114-115, IRSNB mys3623-25, 3750-51, 3759, 3820-22, 3859, 3861-75, USNM 566887.
27. St. Matthias: Mussau [-1.4315 149.6111], SMF 08206-207, ZMB 26473.
28. St. Matthias: Emirau Island [-1.6572 149.9659], MVZ 40779-783, USNM 120881.
29. New Hanover: Taskul [-2.5669 150.4164], no specimens.
30. New Ireland [-4.4788 152.7605], AMNH 104967, 104974-975, 104978, 104980, 104982, 104984, 104986-991, 104994, 104996, BPBM 2580, 11856-858, 11892-893, 11923, 12169-171, MCZ R152836, USNM 518569.
31. New Britain, East [-4.9438 151.8162]: Marmar [-5.4989 151.4893], BPBM 22010, 22012-015, 22017-019, 22021-024, 22026-029, 22031-032; Keravat [-4.3551 152.04697], BPBM 24128, SAM R8505-12, R8692-97; Rabaul [-4.1998 152.164], FMNH 13861, 13864; Mount Sinewit [-4.633 152.753], BPBM 2296.
32. New Britain, West [-5.8152 149.8374]: Kandrian [-6.2055 149.5495], SAM R7465; Talasea [-5.2738 150.0088], AMNH 105505-518, SAM R6720, R6724, R6733, R6735, R6743; Hoskin [-5.4617 150.4040], AMNH 117744-745.
33. Bougainville [-6.1074 155.1822]: Mutah [-5.6659 154.9638], CAS 110143, 110146-149, 110152, 110154; Boskombo (=Boskambo) [-5.6599 155.0942], BPBM 16983-986, 16988-993, 16995-998, BPBM-McCoy 05, 07-08, 22 62-67, A-D; Teopasino Plantation [-5.6400 155.0989], BPBM 16999-17000, BPBM-McCoy 108-109; Torokina [-6.2269 155.0620], USNM 119817, 119820, 119823, 119825, 119827; Cape Torokina [-6.2475 155.0407], USNM 120138-140; Pamauita [-6.6042 155.6319], CAS 110391-394; Matsiogu [-6.6332 155.6337], CAS 11206.
34. Morobe coast (Kamiali) [-7.2950 147.1114], BPBM 25964-965, 25967-969, 25971, 31468-469, PNGAA 17181, USNM.RNF 8919-21.
35. Mount Lamington [-8.9409 148.1579], AMS R9360A-B.
36. Popondetta [-894.09 148.1579], USNM 195672.
37. Collingwood Bay area [-9.5248 149.2955]: Mount Dayman [-9.7948 149.2741], AMNH 74348; Biniguni [-9.6417 149.3041], AMNH 74107; Kwagiri River [-9.5828 149.4321], AMNH 74335-336, 74383; Menapi [-9.7603 149.9328], AMNH 74317, 74210.
38. Goodenough Island (D'Entrecasteaux Islands) [-9.3368 150.2465], AMS R74279, R74281, MCZ R146095-099.
39. Fergusson Island (D'Entrecasteaux Islands) [-9.5325 150.6779], AMS R76733, BPBM 15854-869, 15874-884.
40. Normandy Island (D'Entrecasteaux Islands) [-10.0405 151.0249], AMNH 76733, AMS R12795, R129802, R129804-807, R129812-14, R129852, BPBM 15843, 15885-886, 16759-760.
41. Kiriwina (Trobriand Islands) [8.5042 151.0762], AMS R86843-849; Kuia [no geocoordinates located], AMS R102950-952, R102967-969, USNM 192984-985, 325068-080.
42. Egum Atoll: Yanaba Island [-9.2696 151.8965], BPBM 16837-839.
43. Woodlark Island [-9.1272 152.7945], BPBM 17680-681, 17683.
44. Panaeti, Conflict Group (Louisiade Archipelago) [-10.6851 152.3727], AMS R4777-4779.
45. Misima (Louisiade Archipelago) [-10.6715 152.7480], BPBM 16739-758.
46. Sudest, Sudest Island (Louisiade Archipelago) [-11.5214 153.4996], BPBM 19831-838, 19840, 19843, 19845-849, 1852-854.
47. Nimowa [-11.3054 153.2521], BPBM 19881-885.
48. Rossel-Yela (Louisiade Archipelago) [-11.3545 154.1862], AMNH 76752, BPBM 21135, 19864-885.
49. Milne Bay: lowlands [-10.3293 150.3104], AMS R124906, BPBM 6146, LSUMZ 96321, 93326-327, 96333-335, 123532, MCZ R14096-099, USNM 159816; Kinahidamana River at Alotau [-10.2988 150.4282], BPBM 15663-664, 15848-849, 15851-852; tip of East Cape [-10.2301 150.8745], LSUMZ 93316.
50. Milne Bay: East Cape mountains [-10.2888 150.5233], LSUMZ 93318-320; Halowia [-10.3356 150.5730], LSUMZ 93307-312, 96323, 96327, 96332, 123535; Nadue [-10.3136 150.6222], BPBM 15850.
51. Milne Bay: Owen Stanley mountains, Duabo [-10.4184 150.3068], BPBM 15448-449; Pini range [-10.4080

- 150.5072], LSUMZ 96260–262, 96338, 96342, 96263–264, 123535, 123537, 123550; Mount Pekopekowana [–10.2851 150.1882], BPBM 15450–452.
52. Milne Bay: Sideia and nearby islands [–10.5863 150.2910], AMS R129507–508; Kwatto [–10.614 150.632], USNM 119177.
53. Milne Bay: Fife Bay [–10.60 150.00], AMS R8547, R8549; Lahimona [–10.4199 150.0620], LSUMZ 93330, 96265, 123547, 123551, 123553–556; Takwatakwi [–10.3993 150.0916], LSUMZ 93329–330, 96266–271, 123547, 123533–534, 133536, 123557–558.
54. Milne Bay: southern mountains [–10.6130 150.2910], Bwaona River [–10.5039 150.3042], BPBM 15443; Cloudy Mountain [–10.5565 150.2168], BPBM 15444–447, LSUMZ 123537.
Milne Bay alphabets: A, BPBM 15443, 15448–452; B, BPBM 15663–664, 15848–852, 1850; C, LSUMZ 123532–533, 123535, 123537, 123550; D, LSUMZ 93330, 96265, 96260–264, 96266–271, 96278, 123534, 123547, 123551, 123553–555, 123557–558.
55. Central Province, mountains [–9.444 147.984]: Mount Derobison [–9.4625 147.92], BPBM 18687; Laronu [–9.4439 147.984], BPBM 19511; Wori [–9.3931 147.55797], BPBM 27661–665, 27667–672.
56. Central Province: Port Moresby area savanna [–9.4349 147.2128], AMNH 103245–246, 103249, 103252–254, 103457, AMS R24378, R69459–462, R126048, UMMZ 127135; Rigo Road [–97997 147.5261], FLMNH 43455–457, USNM 212978; Jackson Airport [–9.4400 147.2178], USNM 212978; Boroko [–9.4694 147.1996], CAS 118198, USNM 195670–671; Moitaki [–9.4277 147.1904], FLMNH 43452–453, 43458, 44029, 44031, USNM 212979–980, 212982, 212984–987; Wagani [–9.4194 147.1858], CAS 118035–038.
57. Central Province: Port Moresby area forest [–9.4349 147.2128], McDonald USNM 212972; Owen's Corner USNM 212971; Rouna [–9.4268 147.3898], CAS 118000–001, MCZ R101547–549, R101551–552, R101554–558; Laloki River [–9.1999 147.2337], AMS R14585, 14597, R14632–637, USNM 212972–977; Brown River [–9.1610 147.1566], FLMNH 43451, UMMZ 131269.
58. Central Province: Kairuku (Yule Island) [–8.8201 146.5297], AMS R31934, USNM 195674, 325082–083.
59. Gulf coast: Morobe Province, Tekadu [–7.66485 146.56385], BPBM 13173, 13175–177, USNM 518568.
60. Gulf coast: Purari River [–7.4454 144.6976], Orlo (=Orloli?) [–7.4020 145.1965], CAS 117966, 117970, 117972, 117974, 1179976–978; Piu (=Pio) River [–6.7351 144.7926], CAS 118008, 118010; Uraru [–6.8925 144.3553], CAS 117979, 118023, 118026, 118028, 118032, MCZ R101622–635, USNM 192414–418.
61. Gulf coast: Kikori [–7.4454 144.6976], Airdhill [–7.4158 144.3553], ZSM 206–207, 251–260.
62. Highlands: Chimbu [–6.3088 144.8731], BPBM 18957, 28264–265, USNM 518567.
63. Highlands: South [–6.0202 143.4008], Waro AMS R122391–392.
64. Western Province: Emeti area [–7.8600 143.2448], Adiba [–8.0746 142.8772], MCZ R123212, Emeti USNM 195757, 325059–066.
65. Western Province: south central (Lake Murray area) [–6.9068 141.4994], MCZ R124313.
66. Western Province: southwest (“Wipim” peninsula) [–8.7914 142.88954], Boze [–9.0618 143.0397], MCZ R124299; Wipim [–8.7914 142.88954], AMS R121165, MCZ R14115, R14117–119, R41122–125, R41127–130, R41132–133.
67. Lorentz River: Sabang (not located) [–4.6272 137.9720], ZMA 15379.
68. Eilander River: Wamena [–4.0941 138.9450], BMNH 1978.2180.
69. Kei Islands (*undulatus* and Elat) [–5.6575 132.9915], RMNH 5095.
- TS. Torres Strait Islands [–10.0927 142.5037; see Zug, 1998: fig. 5], AMS R36578, R38528, R42555, R44230, R44270, R45080, R45904, R45909–910, R45957–958, R46504–507, R46138, R48998–999, R58976, R59019, R59118, R130678–679.

Appendix C: Species Identification of Individuals Examined

ASSIGNED

- Nactus aktites* (PNG north coast): IRSNB 16456A–G, 16526.1380, 16526.1383.
- N. allenallisoni* (PNG north coast): AMNH 100059, 104873–877, 105023, 105026, 105029; AMS R31260–262, R31262, R31268, R31272–273, R31278, R31281–284, R31291–292, R31297, R124018–027, R124029–030, R124052; BPBM 05806, 13173, 13175–177, 24066–068, 24071, 31467, JW12, JW18–19, JW48; CAS 126710–711, 126713, 134376–378, 192824, 192887–288, 192903; MCZ R101533, R124293–295, R124302–304; RMNH 8831A–C; USNM 119176, 119234–238, 159915–919, 518568, 566875–876, 566881–882. Hybrid: AMS R124028.
- N. alotau* (PNG SE and S coast): AMS R8547, R8549, R124906, R129508; BPBM 06146, 15444–447, 15663–664, 15848–852, 18687, 19511, 27661–665, 27667–672; LSUMZ 93307–312, 93316, 93318–320, 93326–327, cca4289–90, 4294, 4355, 4420, 4422, 4424, 4444, 4734, 4747–4749, 4865, 4869; MCZ R1466096–099; USNM 159816.
- N. amplus* (Sudest Island): BPBM 19846, 19848, 19864–865, 19867, 19869.
- N. arceo* (Morotai): BYU 7331, 7540.
- N. arfakianus* (Schouten Islands): BPBM 3951; UMMZ 122449.
- N. chrisaustini* (Milne Bay mainland): LSUMZ 123532, 1235535, 123550.
- N. erugatus* (Owen Stanley terminus, Milne Bay): BPBM 15443, 15448–452.
- N. fredkrausi* (Misima Island): BPBM 16739–756, 16758.
- N. grevifer* (Torricelli Mountains and Bom): IRSNB 15802A–802S, 15871.1373, 15871.1379–1380, 15871.1383–1385, 15871.1387.
- N. heteronotus* (Central Province savanna): AMNH 103245–246, 103249, 103457; AMS R31934, R69453–462; CAS 118035, 118038, 118198; UF 43452–453, 43455–458, 44029, 44031; UMMZ 127135; USNM 195670–671, 195674, 212978–982, 212980, 212984–987.
- N. intrudusus* (Markham Valley): AMNH 66731–732, 92664, 95175–177, 95653, 103242–243; AMS R13255; MCZ R98759; SAM 03671.
- N. inundatus* (southwest PNG and southeast Papua): AMS R121165, R122391–392; BMNH 1978.2180; BPBM 18957, 28264–265; MCZ R123212, R124299, R124313, R141115, R141117–119, 141122–125, 141127–130, R141132–133; USNM 325059–066, 518567; ZMA 15379.
- N. kamiali* (northeast PNG coast): AMS R93660A–60B; BPBM 25964–969, 25971, 31468–469; CAS 249851; PGNA 17181; RNF 8921; USNM 195672, 576310.
- N. kunan* (Manus Island): PNGNM 25190; USNM 576300.

- N. modicus* (Sudest/Sudest and Rossel Islands): BPBM 19831–834, 19845, 19847, 19849, 19852–854, 19870–876, 19878–885, 21135.
- N. nanus* (northern PNG coast): AMS R124051, R124053.
- N. notios* (southern mountains, Milne Bay): LSUMZ 93330, cca4269, 4286–88, 4291–93, 4295–4299, 4301, 4303, 4445–46, 4625, 4628, 5060, 5073.
- N. panaeati* (Panaeati Island): AMS R4777–4779.
- N. papua* (Kikori and Purari drainages): CAS117966, 117970, 117974, 117976–979, 118008, 118010, 118023, 118026, 118028, 118032; MCZ R101622–635; USNM 192414–418; ZSM 206–207, 251–260.
- N. papua* (Torres Strait Islands): AMS R36578, R38528, R42555, R44230, R44270, R45080, R45904, R45909–910, R45957–958, R46504–507, R46138, R48998–999, R58976, R59019, R59118, R130678–679.
- N. pelagicus* (Bougainville): BPBM 16983–986, 16988–17000; USNM 1201380–140.
- N. pelagicus* (Manus): AMS R29071–74, 31114–115; IRSNB mys3623–65, mys3750–51, mys3820–22, mys3859, mys61–75; USNM 566887.
- N. rainerguentheri* (assuming most of Vogelkop): ZMB 62760.
- N. robertfisheri* (Bismarck Archipelago and Bougainville): AMNH 104967, 104974–75, 104978–91, 104994, 104996, 105006–018, 117744–745; BPBM 2580, 11856–58, 11892–93, 11923, 12169–171, 22010, 22012–015, 22017–019, 22021–024, 22026–029, 22031–032, 24128; CAS 94001, 110143, 110146–149, 110152, 110154, 110206, 110391–394; FMNH 13861, 13864; MVZ 40779–783; SAM 6720, 6724, 6733, 6735, 6743, 7465, 8505–06, 8508–09, 8692–93, 8695–97; SMF 08207A–B; USNM 119817, 119820, 119823, 119825, 119827; ZMB 26473.
- N. septentrionalis* (north coast Indonesia Papua and PNG): AMNH 105023, 105025, 105028, 100056–058, 100060–062; BPBM AA13612, 6156, 18954–956, 23360–062; MCZ R49264–268, R153031, RMNH 8831D; USNM 119239–240; ZMA 15378; ZMB 58589–590.
- N. undulatus* (Kai): RMNH 5095.

NOT ASSIGNED

- Collingwood Bay area (sample 37): AMNH 74107, 74137, 74210, 74335–336, 74348, 74348.
- D'Entrecasteaux Islands (38, 39): AMS R47279, R74281; BPBM 15854–863, 15865–869, 15874–884; MCZ R146095–099.
- Normanby Island (40): AMNH 76733, AMS R129795, R129802, R129804–807, R129812–14, R129852; BPBM 15853, 15885–886, 16759–760.
- Trobriand Group (41): AMS R86843–849, R102950–952, R102967–69; BPBM 16837–839, 17680–681, 17683; USNM 192984–985, 325068–076.

References

- Allison, A. 1996. Zoogeography of Amphibians and Reptiles of New Guinea and the Pacific Region. In *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes*, ed. A. Keast and S. E. Miller, pp. 407–336. Amsterdam: SP Academic Publisher.
- Allison, A., and S. Leisz. 2009. Analysis of the Impacts of Climate Change on the Herpetofauna of the Papuan Region (New Guinea to the Solomon Islands). Honolulu: Bishop Museum.
- Austin, C. A., M. Spartaro, S. Peterson, J. Jordan, and J. D. McVay. 2011. Conservation Genetics of Boelen's Python (*Morelia boeleni*) from New Guinea: Reduced Genetic Diversity and Divergence of Captive and Wild Animals. *Conservation Genetics*, 11:889–896. <https://doi.org/10.1007/s10592-009-9931-z>
- Baldwin, S. L., P. G. Fitzgerald, and L. E. Webb. 2012. Tectonics of the New Guinea Region. *Annual Review of Earth and Planetary Sciences*, 40:495–520. <https://doi.org/10.1146/annurev-earth-040809-152540>
- Bauer, A., and R. Günther. 1991. An Annotated Type Catalogue of the Geckos (Reptilia: Gekkonidae) in the Zoological Museum, Berlin. *Mitteilungen der zoologische Museum Berlin*, 67(2):279–310. <https://doi.org/10.1002/mmz.19910670204>
- Boulenger, G. A. 1885. *Catalogue of the Lizards in the British Museum (Natural History)*. Volume 1: *Gekkonidae, Eublepharidae, Uroplatidae, Pygopodiadae, Agamidae*. 2nd ed. London: Printed by Order of the Trustees.
- Brongersma, L. D. 1933. A New Gecko of the Genus *Gymnodactylus* from New Guinea. *Annals and Magazine of Natural History*, ser. 10, 11:252–253. <https://doi.org/10.1080/00222933308673654>
- Brongersma, L. D. 1948. Lizards from the Island of Morotai (Moluccas). *Koninklijke Nederlandsche Akademie van Wetenschappen, Proceedings*, 51:486–495.
- Brown, W. C. 1991. Lizards of the Genus *Emoia* (Scincidae) with Observations on Their Evolution and Biogeography. *Memoirs of the California Academy of Sciences*, 15:i–vi, 1–94.
- Brown, W. C., and F. Parker. 1973. A New Species of *Cyrtodactylus* (Gekkonidae) from New Guinea with a Key to Species from the Island. *Breviora*, 417:1–7.
- de Rooij, N. 1915. *The Reptiles of the Indo-Australian Archipelago*. Volume 1: *Lacertilia, Chelonia, Emydosauria*. Leiden: E. J. Brill. <https://doi.org/10.5962/bhl.title.5069>
- Donnellan, S. C., K. P. Aplin, and T. Bertozzi. 2010. Species Boundaries in the *Rana arfaki* Group (Anura: Ranidae) and Phylogenetic Relationships to Other New Guinea *Rana*. *Zootaxa*, 2496:49–62. <https://doi.org/10.11646/zootaxa.2496.1.3>
- Donnellan, S. C., and C. Moritz. 1995. Genetic Diversity of Bisexual and Parthenogenetic Populations of Tropical Gecko *Nactus pelagicus* (Lacertilia: Gekkonidae). *Herpetologica*, 51:140–154.
- Duméril, A. 1856. Description des reptiles nouveaux or imparfaitement connus de la collection du Muséum d'Histoire naturelle et remarques sur la classification et les caractères des reptiles. *Archive de Muséum d'Histoire Naturelle*, 8:437–588.
- Duméril, A. M. C., G. Bibron, and A. H. A. Duméril. 1856. *Erpétologie générale, ou Histoire naturelle complète des reptiles*. Paris: Librairie Encyclopédique de Roret.
- Duméril, C., and A. Duméril. 1851. *Catalogue Méthodique de la Collection des Reptiles du Muséum d'Histoire Naturelle de Paris*. Paris: Gide et Baudry Libraires-Éditeurs.
- Eckstut, M. E., A. M. Hamilton, and C. A. Austin. 2013. Variable Unisexuality and Uniform Bisexuality: Morphology, Genetics, and Biogeography of the *Nactus pelagicus* Complex on Tanna Island, Vanuatu. *Herpetologica*, 69:199–213. <https://doi.org/10.1655/HERPETOLOGICA-D-11-00089>
- Eckstut, M. E., A. M. Hamilton, C. C. Austin, and D. M. Sever. 2009. Asynchronous Oviductal Seasonal Variation in the Unisexual-Bisexual *Nactus pelagicus* Complex from the Vanuatu Archipelago (Reptilia: Squamata: Gekkonidae). *Animal Reproduction: New Research Developments*, 2009:295–307.
- Frost, D. 2019. Amphibian Species of the World, an Online Reference. <http://research.amnh.org/vz/herpetology/amphibia/> (accessed 13 July 2019).

- Girard, C. 1857. Description of Some New Reptiles, Collected by the United States Exploring Expedition, under the Command of Capt. Charles Wilkes, U.S.N. Fourth Part: Including the Species of Saurians, Exotic to North America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 9:194–199.
- Günther, A. 1872. On Some New Species of Reptiles and Fishes Collected by J. Brencley, Esq. *Annals and Magazine of Natural History*, ser. 4, 10:418–426. <https://doi.org/10.1080/00222937208696731>
- Günther, A. 1873. Reptiles. In *Jottings during the Cruise of H.M.S. Curacoa among the South Sea Islands in 1865*, by J. L. Brencley, pp. 395–408. London: Longmans, Green.
- Heinicke, M. P., E. Greenbaum, T. R. Jackman, and A. M. Bauer. 2010. Molecular Phylogenetics of Pacific *Nactus* (Squamata: Gekkota: Gekkonidae) and the Diphyly of Australian Species. *Proceedings of the California Academy of Sciences*, ser. 4, 61:633–646.
- Heinsohn, T., and G. Hope. 2006. The Torresian Connections: Zoogeography of New Guinea. In *Evolution and Biogeography of Australasian Vertebrates*, ed. J. R. Merrick, M. Archer, G. M. Hickey, and M. S. Y. Lee, pp. 71–93. Oatlands, NSW, Australia: Auscipub.
- Horner, P. 2007. Systematics of the Snake-Eyed Skinks, *Cryptoblepharus* Wiegmann (Reptilia: Squamata: Scincidae) – an Australian-Based Review. *The Beagle, Records of the Museum and Art Galleries of the Northern Territory, Supplement*, 3:21–198.
- Ingram, G. J. 1978. A New Species of Gecko, Genus *Cyrtodactylus*, from Cape York Peninsula, Queensland, Australia. *Victorian Naturalist*, 95:142–146.
- International Commission on Zoological Nomenclature (ICZN). 1991. Opinion 1647. *Heteronota pelagica* Girard, 1857 (Currently *Gymnodactylus*, *Cyrtodactylus* or *Nactus pelagicus*; Reptilia, Sauria): Given Precedence over *Gymnodactylus amouxi* Duméril, 1851. *Bulletin of Zoological Nomenclature*, 48:185–187.
- Jackman, T. R., A. M. Bauer, and E. Greenbaum. 2008. Phylogenetic Relationships of Geckos of the Genus *Nactus* and Their Relatives (Squamata: Gekkonidae). *Acta Herpetologica*, 3:1–18.
- Kaiser, C. M., H. Kaiser, and M. O'Shea. 2018. The Taxonomic History of Indo-Papuan Groundsnakes, Genus *Stegonotus* Duméril et al., 1854 (Colubridae), with Some Taxonomic Revisions and the Designation of a Neotype for *S. parvus* (Meyer, 1874). *Zootaxa*, 4512:1–73. <https://doi.org/10.11646/zootaxa.4512.1>
- Kaiser, C. M., M. O'Shea, and H. Kaiser. 2019. A New Species of Indo-Papuan Groundsnake, Genus *Stegonotus* Duméril et al., 1854 (Serpentes, Colubridae), from the Bird's Head Peninsula of West Papua, Indonesia, with Comments on Differentiating Morphological Characters. *Zootaxa*, 4590:1–73. <https://doi.org/10.11646/zootaxa.4590.2.1>
- Karin, B. R., A. L. Stubbs, U. Arifin, L. M. Bloch, G. Ranadhan, D. T. Iskandar, E. Arida, S. B. Reilly, A. Kusnadi, and J. A. McGuire. 2018. The Herpetofauna of the Kei Islands (Maluku, Indonesia): Comprehensive Report on New and Historical Collections, Biogeographic Patterns, Conservation Concerns, and an Annotated Checklist of Species from Kei Kecil, Kei Besar, Tam and Kur. *Raffles Bulletin of Zoology*, 66:704–738.
- Kluge, A. G. 1983. Cladistic Relationships among Gekkonid Lizards. *Copeia*, 1983:465–475. <https://doi.org/10.2307/1444392>
- Kluge, A. G. 1989. Comment on the Specific Name (*arnouxii* Duméril, 1851 or *pelagic* Girard, 1857) of a Pacific-Basin Gekkonid Lizard. *Bulletin of Zoological Nomenclature*, 46:46–48. <https://doi.org/10.5962/bhl.part.481>
- Koch, A., E. Arida, A. Riyanto, and W. Böhme. 2009. Islands between the Realms: A Revised Checklist of the Herpetofauna of the Talaud Archipelago, Indonesia, with a Discussion about Its Biogeographic Affinities. *Bonner zoologische Beiträge*, 56(1/2):107–129.
- Köhler, F., and R. Günther. 2008. The Radiation of Microhylid Frogs (Amphibia: Anura) on New Guinea: A Mitochondrial Phylogeny Reveals Parallel Evolution of Morphological and Life History Traits and Disproves the Current Based Morphology-Based Classification. *Molecular Phylogenetics and Evolution*, 47:353–365. <https://doi.org/10.1016/j.ympev.2007.11.032>
- Kopstein, F. 1926. Reptilien von den Molukken und den benachbarten Inseln. *Zoologische Mededeelingen*, 9:71–112.
- Kraus, F. 2005. The Genus *Nactus* (Lacertilia: Gekkonidae): A Phylogenetic Analysis and Description of Two New Species from the Papuan Region. *Zootaxa*, 1061:1–28. <https://doi.org/10.11646/zootaxa.1061.1.1>
- Kraus, F. 2008. Taxonomic Partitioning of *Cyrtodactylus louisianensis* (Lacertilia: Gekkonidae) from Papua New Guinea. *Zootaxa*, 1883:1–27. <https://doi.org/10.11646/zootaxa.1883.1.1>
- Kraus, F. 2012. Papuan Frogs of the Genus *Cophixalus* (Anura: Microhylidae): New Synonyms, New Species, and a Dichotomous Key. *Zootaxa*, 3559:1–36. <https://doi.org/10.11646/zootaxa.3559.1.1>
- Kraus, F. 2013. Three new species of *Oreophryne* (Anura, Microhylidae) from Papua New Guinea. *ZooKeys* 333:93–121.
- Kraus, F., and A. Allison. 2001. A Review of the Endemic New Guinea Microhylid Frog Genus *Choerophryne*. *Herpetologica*, 57:214–232.
- Kraus, F., and A. Allison. 2004. A New Species of *Tropidonophis* (Serpentes: Colubridae: Natricinae) from the D'Entrecasteaux Islands, Papua New Guinea. *Proceedings of the Biological Society of Washington*, 117(3):303–310.
- Kraus, F., and A. Allison. 2007. Taxonomic Notes on Frogs of the Genus *Rana* from Milne Bay Province, Papua New Guinea. *Herpetological Monographs*, 21:33–75. <https://doi.org/10.1655/06-004.1>
- Kraus, F., and S. Myers. 2012. New Species of *Hypsilurus* (Squamata: Agamidae) from Papua New Guinea. *Journal of Herpetology*, 46(3):396–401. <https://doi.org/10.1670/11-159>
- Loveridge, A. 1948. New Guinea Reptiles and Amphibians in the Museum of Comparative Zoology and United States National Museum. *Bulletin of the Museum of Comparative Zoology*, 101:307–430.
- Macleay, W. 1878. The Lizards of the “Chevert” Expedition. *Proceedings of the Linnaean Society of New South Wales*, 2:97–104.
- Malnate, E. V., and G. Underwood. 1988. Australasian Natricine Snakes of the Genus *Tropidonophis*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 140:59–201.
- Manthey, U., and W. Denzer. 2016. Melanesian Anglehead Lizards of the Genus *Hypsilurus* Peters, 1867 – Part 1: Species from New Guinea. *Sauria*, 38(3):11–36.
- McCann, C. 1955. The Lizards of New Zealand. Gekkonidae and Scincidae. *Dominion Museum Bulletin*, 17:i–viii, 1–127.
- Menzies, J. 2006. *The Frogs of New Guinea and the Solomon Islands*. Sofia, Bulgaria: Pensoft.
- Metzger, G. A., F. Kraus, A. Allison, and C. L. Parkinson. 2010. Uncovering Cryptic Diversity in *Aspidomorphus* (Serpentes: Elapidae): Evidence from Mitochondrial and Nuclear Markers. *Molecular Phylogenetics and Evolution*, 54:405–416. <https://doi.org/10.1016/j.ympev.2009.07.027>
- Meyer, A. B. 1874. Übersicht der von mir auf Neu-Guinea und den Inseln Jobi, Mysore und Mafoor im Jahre 1873 gesammelten Amphibien. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1874:128–140.
- Meyer, A. B. 1887. Verzeichniss der von mir in den Jahren 1870–1873 im ostindischen Archipel gesammelten Reptilien und Batrachier. *Abhandlungen und Berichte der Königlich Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden*, 1(2):1–16.
- Moritz, C. 1987. Parthenogenesis in the Tropical Gekkonid Lizard, *Nactus pelagicus* (Sauria: Gekkonidae). *Evolution*, 41:1252–1266. <https://doi.org/10.1111/j.1558-5646.1987.tb02464.x>
- Moritz, C., and D. King. 1985. Cytogenetic Perspectives on Parthenogenesis in the Gekkonidae. In *Biology of Australasian Frogs of Reptiles*, ed. G. Grigg, R. Shine, and H. Ehmann, pp. 327–337. Chipping Norton, NSW: Surrey Beatty & Sons.
- Mys, B. 1988. The Zoogeography of the Scincid Lizards from North Papua New Guinea (Reptilia: Scincidae). I. The Distribution of the Species. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie*, 58:127–183.
- Oliver, P., A. Iannela, S. J. Richards, and M. S. Y. Lee. 2017. Mountain Colonisation, Miniaturisation and Ecological Evolution in a Radiation of Direct Developing New Guinea Frogs (*Choerophryne*, Microhylidae). *PeerJ*, 5:e3077. <https://doi.org/10.7717/peerj.3077>
- Oliver, P. M., R. M. Brown, F. Kraus, E. Rittmeyer, S. L. Travers, and C. D. Siler. 2018. Lizards of the Lost Arcs: Mid-Cenozoic Diversification, Persistence and Ecological Marginalization in the West Pacific. *Proceedings of the Royal Society B*, 285:20171760.
- O'Shea, M. 1996. *A Guide to the Snakes of Papua New Guinea*. Port Moresby: Independent Publishing.
- O'Shea, M., A. Allison, and H. Kaiser. 2018. The Taxonomic History of the Enigmatic Papuan Snake Genus *Toxicocalamus* (Elapidae: Hydrophiinae), with the Description of a New Species from the Managalas Plateau of Oro Province, Papua New Guinea, and a Revised Dichotomous Key. *Amphibia-Reptilia*, 39:403–433. <https://doi.org/10.1163/15685381-20181052>
- Peters, W., and G. Doria. 1878. Catalogo dei reptili e dei batraci raccolti da O. Beccari, L. M. D'Albertis e A. A. Brujini nella sotto-regione Austro-Malese. *Annali del Museo Civico di Storia Naturale di Genova*, 13:323–450.
- Rawlings, L. H., and S. C. Donnellan. 2003. Phylogeographic Analysis of the Green Python, *Morelia viridis*, Reveals Cryptic Diversity. *Molecular Phylogenetics and Evolution*, 27:36–44. [https://doi.org/10.1016/S1055-7903\(02\)00396-2](https://doi.org/10.1016/S1055-7903(02)00396-2)
- Reynolds, R. G., and R. W. Henderson. 2018. Boas of the World (Superfamily Booidae): A Checklist with Systematic, Taxonomic, and Conservation

- Assessments. *Bulletin of the Museum of Comparative Zoology*, 162(1):1–58. <https://doi.org/10.3099/MCZ48.1>
- Rhodin, A. G. J., J. B. Iverson, R. Bour, U. Fritz, A. Georges, H. B. Shaffer, and P. P. van Dijk. 2017. *Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status*. 8th ed. Chelonian Research Monograph 7. Lunenburg, Mass.: Chelonian Research Foundation. <https://doi.org/10.3854/crm.7.checklist.atlas.v8.2017>
- Richards, S. J., and K. A. Aplin. 2015. Herpetofauna of Manus and Mussau Islands. In *A Rapid Biodiversity Survey of Papua New Guinea's Manus and Mussau Islands*, ed. N. Whitmore, pp. 31–37. Goroka, Papua New Guinea: Wildlife Conservation Society Papua New Guinea Program.
- Richmond, J. Q., D. A. Wood, J. W. Stanford, and R. N. Fisher. 2014. Testing for Multiple Invasion Routes and Source Populations for the Invasive Brown Treesnake (*Boiga irregularis*) on Guam: Implications for pest Management. *Biological Invasions*, 17:337–349. <https://doi.org/10.1007/s10530-014-0733-y>
- Rivera, J. A., F. Kraus, A. Allison, and M. A. Butler. 2017. Molecular Phylogenetics and Dating of the Problematic New Guinea Microhylid Frogs (Amphibia: Anura) Reveals Elevated Speciation Rates and Need for Taxonomic Reclassification. *Molecular Phylogenetics and Evolution*, 112:1–11. <https://doi.org/10.1016/j.ympev.2017.04.008>
- Rösler, H., F. Glaw, and R. Günther. 2005. Aktualisierte Liste der Geckos von Neuguinea (Sauria: Gekkonidae: Gekkoninae) mit vorläufiger Charakterisierung von neun Formen aus den Gattungen *Cyrtodactylus* Gray, 1827, *Gebysa* Gray, 1834 und *Nactus* Kluge, 1983. *Gekkota*, 5:33–64.
- Ruane, S., S. J. Richards, J. D. McVay, B. Tjaturadi, K. Krey, and C. C. Austin. 2018. Cryptic and Non-cryptic Diversity in New Guinea Ground Snakes of the Genus *Stegonotus* Duméril, Bibron and Duméril, 1854: A Description of Four New Species (Squamata: Colubridae). *Journal of Natural History*, 52:767–770. <https://doi.org/10.1080/00222933.2017.1391959>
- Sabaj Pérez, M. H., ed. 2010. Standard Symbolic Codes for Institutional Resource Collections in Herpetology and Ichthyology: An Online Reference, Version 2.0. <http://www.asih.org> (accessed 8 November 2010).
- Schleip, W. D. 2008. Revision of the Genus *Leiopython* Hubrecht 1879 (Serpentes: Pythonidae) with the Redescription of Taxa Recently Described by Hoser (2000) and the Description of New Species. *Journal of Herpetology*, 42(4):645–667. <https://doi.org/10.1670/06-182R5.1>
- Schleip, W. D. 2014. Two New Species of *Leiopython* Hubrecht, 1879 (Pythonidae: Serpentes): Non-compliance with the International Code of Zoological Nomenclature Leads to Unavailable Names in Zoological Nomenclature. *Journal of Herpetology*, 42(4):645–667. <https://doi.org/10.1670/06-182R5.1>
- Schwaneer, T. 1980. Reproductive Biology of Lizards on the American Samoan Islands. *Occasional Papers of the Museum Natural History, the University of Kansas*, 86:1–53.
- Shine, R., C. L. Spencer, and J. S. Keogh. 2014. Morphology, Reproduction and Diet in Australian and Papuan Death Adders (*Acanthopphis*, Elapidae). *PLoS ONE*, 9(4):e94216. <https://doi.org/10.1371/journal.pone.0094216>
- Tallowin, O. J. S., A. Allison, A. C. Algar, F. Kraus, and S. Meiri. 2017. Papua New Guinea Terrestrial-Vertebrate Richness: Elevation Matters Most for All Except Reptiles. *Journal of Biogeography*, 44:1734–1744. <https://doi.org/10.1111/jbi.12949>
- Tan, H. H. 2016. Commensal Herpetofauna at Tufi Resort, Oro Province, Papua New Guinea. *Southeast Asia Vertebrate Records*, 2016, [https://www.ecology-asia.com/pdf/2016/seavr2016-054\(p127-128\).pdf](https://www.ecology-asia.com/pdf/2016/seavr2016-054(p127-128).pdf) (accessed 12 June 2020).
- Tanner, V. M. 1950. Pacific Islands Herpetology No. III: Morotai Island. *Great Basin Naturalist*, 10:1–30. <https://doi.org/10.5962/bhl.part.10362>
- Uetz, P., P. Freed, and J. Hošek, eds. 2019. The Reptile Database. <http://reptile-database.org> (accessed 20 March 2019).
- Wüster, W., A. J. Dumbrell, C. Hay, C. E. Pook, D. J. Williams, and B. G. Fry. 2005. Snakes across the Strait: Trans-Torresian Phylogeographic Relationships in Three Genera of Australasian Snakes (Serpentes: Elapidae: *Acanthopphis*, *Oxyuramus*, and *Pseudechis*). *Molecular Phylogenetics and Evolution*, 33:1–14. <https://doi.org/10.1016/j.ympev.2004.08.018>
- Zug, G. R. 1985. Pacific Island Lizards—Status of Type Specimens from the U.S. Exploring Expedition 1838–1842. *Copeia*, 1985:150–154. <https://doi.org/10.2307/1444804>
- Zug, G. R. 1989. *Heteronota pelagica* Girard, 1857 (Currently *Gymnodactylus*, *Cryptodactylus* [sic], or *Nactus pelagicus*; Reptilia, Sauria): Proposed Conservation of the Specific Name. *Bulletin of Zoological Nomenclature*, 46:38–40.
- Zug, G. R. 1998. Australian Populations of the *Nactus pelagicus* Complex (Reptilia: Gekkonidae). *Memoirs of the Queensland Museum*, 42:613–626.
- Zug, G. R. 2004. Systematics of the *Carlia* “*fusca*” Lizards (Squamata: Scincidae) of New Guinea and Nearby Islands. *Bishop Museum Bulletins in Zoology*, 5:i-viii, 1–154.
- Zug, G. R., and R. N. Fisher. 2012. A Preliminary Assessment of the *Nactus pelagicus* Species Group (Squamata: Gekkonidae) in New Guinea and a New Species from the Admiralty Islands. *Zootaxa*, 3257:22–37. <https://doi.org/10.11646/zootaxa.3257.1.2>
- Zug, G. R., and B. R. Moon. 1995. Systematics of the Pacific Slender-Toed Geckos, *Nactus pelagicus* Complex: Oceania, Vanuatu, and Solomon Island Populations. *Herpetologica*, 51:77–90.
- Zweifel, R. G. 1972. A Review of the Frog Genus *Lechriodus* (Leptodactylidae) of New Guinea and Australia. *American Museum Novitates*, 2507:1–41.

Index of Scientific Names

- Acanthophis*, 76
 laevis, 76
 rugosus, 76
Agamidae, 74
Aspidomorphus, 75–76
 lineatocollis, 76
 muelleri, 76
 schlegeli, 76
Asterophrys turpicola, 73
- Boidae (Candoiidae), 75
Boiga, 75
 irregularis, 75, 76
Bothrochilus, 75
 albertisii, 75
 boa, 75
 fredparkeri, 75
 huonensis, 75
 meridonalis, 75
 montanus, 75
- Candoia*, 75
 aspersa, 75
 carinata, 75
 paulsoni, 75
 paulsoni mcdowellii, 75
 paulsoni rosadoi, 75
 paulsoni sadlieri, 75
Candoiidae (Boidae), 75
Carettochelys, 74
Carlia, 74
 aenigma, 74
 aramia, 74
 beccarii, 74
 eothen, 74
 fusca, 74
 luctuosa, 74
 mysi, 74
 pullum, 74
Ceratobatrachidae, 73
- Ceratophryidae, 72
Choerophryne, 72, 73
 proboscidea, 73
Colubridae, 75
Cophixalus, 72
 balbus, 73
 cupricarenum, 73
 riparius, 73
 variabilis, 73
 verrucosus, 73
Cornufer, 73
 papuensis, 73
Crinia, 73
 remota, 73
Crocodylus
 halli, 73
 novaeguineae, 73
Cryptoblepharus, 74
 keiensis, 74
 richardsi, 74
 yulensis, 74
Cyrtodactylus, 1, 2, 3, 74
 boreoclivus, 74
 equestris, 74
 klugei, 74
 loriae, 74
 louisianensis, 74
 mimikanus, 74
 murua, 74
 novaeguinea, 74
 pelagicus, 3
 rex, 74
 robustus, 74
 seromowaiensis, 74
 tripartitus, 74
 vankampeni, 3
- Dendrelaphis*, 75
 calligaster, 75
 gastrostictus, 75

- Dendrelaphis* (continued)
lineolatus, 75
macrops, 75
punctulatus, 75
Dibamidae, 74
Dibamus novaeguineae, 74
Dicroglossidae, 72, 73
Dixonius, 26
- Elapidae, 75–76
Elseya schultzei, 74
Emoia, 74–75, 76
atrocostata, 75
battersbyi, 75
bismarkensis, 75
brongersmai, 74
caeruleocauda, 75
digul, 74
jakati, 75
kitchneri, 75
loveridgei, 75
mivarti, 75
physicae purari, 74–75
popei, 75
submetallica, 75
tetrataenia, 75
tropidolepis, 74
Emydura subglobosa, 74
- Fejervarya*, 73
- Gehyra*, 74
baliola, 74
dubia, 74
mutilata, 74
oceanica, 74
papuana, 74
rohan, 74
- Gekko*, 74
monarchus, 74
vittatus, 74
- Gekkonidae, 74
Gekkoninae, 37–72
Gekkonini, 3
- Gymnodactylus*, 1, 2, 3
arfakianus, 2, 31
arnouxii, 1
arnouxii, 2, 3, 49
cheverti, 2
heteronota, 31
heteronotus, 2, 65
multicarinatus, 2
pelagicus, 2, 3
pelagicus undulatus, 2, 3, 31, 36, 71
vankampeni, 2
- Gymnodactylus* (Heteronota)
arfakianus, 2, 31, 39
- Heteronota, 2, 26
eboracensis, 2
fasciata, 2, 31, 65
fasciatus, 2
marmorata, 2
pelagica, 1–2, 49
- Hylidae, 72, 73
Hylophorbus, 72
Hypsilurus, 74
auritus, 74
binotatus, 74
geelvinkianus, 74
godeffroyi, 74
magnus, 74
modestus, 74
nigrigularis, 74
papuensis, 74
tenuicephalus, 74
- Lechriodus*, 73
aganoposis, 73
melanopyga, 73
platyceps, 73
- Lepidodactylus*, 74
browni, 74
guppyi, 74
lugubris, 74
magnus, 74
orientalis, 74
pulcher, 74
woodfordi, 74
- Lialis*
burtoni, 74
jicari, 74
- Liasis papuanus*, 75
Limnodynastes, 73
Limnunctes, 73
grummiens, 73
- Litoria*, 73
bibonius, 73
bicolor, 73
flavescens, 73
infrafnata, 73
rubella, 73
- Lycodon capucinus*, 75
- Microhylidae, 72–73
Micropechis ikabeke, 76
Mixophyes, 73
Morelia viridis, 75
- Myobatrachidae, 72, 73
- Nactus*, ix–x, 1–4, 6, 16, 17, 18, 22, 24, 25, 26, 27–32, 34–35, 37, 38, 53, 72–75, 76
acutus, 4, 26, 36, 72
aktites, 32, 38, 45, 47, 72, 74, 75, 85
allenallisoni, 32, 33, 38, 42–43, 44, 45, 47, 72, 73, 74, 75, 85
alotau, 34, 36, 38, 53, 64–65, 67, 72, 73, 75, 85
amplus, 34, 38, 53, 58–60, 72, 73, 74, 85
arceo, 37, 38, 39, 85
arfakianus, 2, 31, 38, 39, 40, 72, 73, 85
arnouxii, 3, 31, 49
- cheverti*, 3, 4, 6, 7, 26, 32, 36, 37
cheverti group, 36, 37
chrisaustini, 34, 35, 38, 53, 60–61, 72, 85
coindemirensis, 4
eboracensis, 3, 4, 6, 7, 26, 32, 36, 67, 69
eboracensis group, 36–37
erugatus, 34, 38, 53, 62–64, 72, 85
fredkrausi, 34, 38, 53, 54–56, 72, 74, 75, 85
galgajuga, 1, 3, 4, 26, 32, 33, 36, 37, 48, 49, 72
grevifer, 32, 38, 43–44, 47, 72, 85
heteronotus, 35, 38, 65–67, 72, 74, 85
intrudusus, 32, 34, 38, 47–48, 72, 74, 75, 76, 85
inundatus, 36, 38, 39, 69–71, 72, 73, 74, 85
kamiali, 33–34, 38, 51–54, 72, 74, 75, 76, 85
kunan, 4, 26, 32, 33, 36, 37, 47, 48–49, 72, 74, 85
modicus, 34, 38, 53, 57–58, 60, 72, 73, 74, 86
multicarinatus, 3, 4, 7, 26, 27, 28, 31, 32, 33, 36, 38
multicarinatus group, 36
nanus, 38, 43, 45–47, 72, 86
notios, 34, 38, 53, 61–62, 72, 86
panaeati, 34, 38, 53, 56–57, 72, 86
papua, 36, 38, 67–69, 70–71, 72, 74, 75, 86
pelagicus, ix–x, 1, 2, 3, 4, 6, 7–26, 28, 31, 32, 33, 36, 47, 49, 72, 74, 75, 86
pelagicus group, 1, 2, 4, 7, 9–12, 13–16, 19–22, 23, 25–26, 31, 36
pelagicus undulatus, 2, 8
rainerguentheri, 38, 39–41, 72, 73, 86
robertfisheri, 33, 38, 50–51, 72, 74, 75, 86
septentrionalis, 31, 32, 38, 39, 41–42, 43, 47, 71, 72, 73, 74, 75, 86
serpensinsula, 1, 3, 4
sphaerodactylodes, 3–4, 26, 36, 72
undulatus, 38, 39, 67, 71, 72, 74, 86
vankampeni, 1, 2, 3–4, 26, 32, 36, 72
vankampeni group, 26, 36
- Nyctimystes*, 73
cheesmanae, 73
humeralis, 73
- infrafnatus*, 76
perimetri, 73
- Oreophryne*, 72
Oxyuranus scutellatus, 76
- Papuarana*, 76
Papurana, 73
arfaki, 73
daemeli, 73
garritor, 73
milneana, 73
papua, 73
supragrisea, 73
waliesae, 73
- Pseudechis*, 76
papuanus, 76
- Pygopodidae, 74
Pythonidae, 75
- Ranidae, 72, 73
Ranoidea, 73
auae, 73
caerulea, 73
impura, 73
- Scincidae, 74
Simalia
amethystina, 75
boeleni, 75
Sphenomorphus, 74
Stegonotus, 75
admiraltiensis, 75
diehli, 75
guentheri, 75
keyensis, 75
parva, 75
poechi, 75
reticulatus, 75
- Toxicocalamus*, 75–76
holopelturus, 76
longissimus, 76
mintoni, 76
misimae, 76
nigrescens, 76
- Tropidonophis*, 75
doriae, 75
hypomelas, 75
mairii, 75
multiscutellatus, 75
- Varanidae, 74
Varanus, 75
doreanus, 75
douarrha, 75
gouldi, 75
indicus, 75
panoples, 75
prasinus, 75, 76
salvador, 75
semotus, 75
similis, 75
spinulosus, 75

SUMMARY OF REQUIREMENTS FOR SMITHSONIAN CONTRIBUTIONS SERIES

For comprehensive guidelines and specifications, visit <https://scholarlypress.si.edu>.

ABSTRACTS must not exceed 300 words.

TEXT must be prepared in a recent version of Microsoft Word; use a Times font in 12 point for regular text; be double-spaced; and have 1" margins.

REQUIRED ELEMENTS are title page, abstract, table of contents, main text, and references.

FIGURES must be numbered sequentially (1, 2, 3, etc.) in the order called out; have components lettered consistently (in size, font, and style) and described in captions; include a scale bar or scale description, if appropriate; include any legends in or on figures rather than in captions. Figures must be original and must be submitted as individual TIF or EPS files.

FIGURE FILES must meet all required specifications in the Digital Art Preparation Guide. Color images should be requested only if required.

TAXONOMIC KEYS in natural history manuscripts should use the aligned-couplet form for zoology. If cross-referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

SYNONYMY IN ZOOLOGY must use the short form (taxon, author, year:page), with full reference at the end of the manuscript under "References."

REFERENCES should be in alphabetical order, and in chronological order for same-author entries. Each reference should be cited at least once in main text. Complete bibliographic information must be included in all citations. Examples of the most common types of citations can be found at SISF's website under Resources/Guidelines & Forms.