Speciation and Dispersal in a Low Diversity Taxon: The Slender Geckos *Hemiphyllodactylus* (Reptilia, Gekkonidae)

George R. Zug

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ABSTRACT

Zug, George R. Speciation and Dispersal in a Low Diversity Taxon: The Slender Geckos *Hemiphyllodactylus* (Reptilia, Gekkonidae). *Smithsonian Contributions to Zoology*, number 631, xi + 70 pages, 25 figures, 7 tables, 2010.—*Hemiphyllodactylus* is a genus of small geckos occurring widely, although uncommonly seen, throughout the Indo-Pacific islands and South Asia. These geckos consist of both bisexual and unisexual species. The unisexual species, *Hemiphyllodactylus typus*, the most widespread of these geckos, apparently attained its Polynesian to Mascarene distribution (invasion) through accidental human transport. The bisexual species have much smaller distributions, geographically restricted to island groups or limited continental areas. Until the early 1990s, most bisexual populations were considered subspecies of *H. typus*. In the last two decades, herpetologists have regularly used species epithets proposed for the region under their investigation. This resurrection of species names has occurred largely without explanation or taxonomic study. This study examines the morphology of *Hemiphyllodactylus* throughout its known range, using 13 regional samples, first examining the differentiation of unisexual and bisexual populations and individuals, then the possibility of regional differentiation among the different bisexual populations. Variation and consistency in morphology in and among the regional sample identify the existence of a wide-ranging unisexual species, *H. typus*, and at least eight geographically restricted bisexual species. Available museum specimens for some regions are adequate to characterize eight bisexual species, *H. aurantiacus*, *H. ganoklonis* n. sp., *H. harterti*, *H. insularis*, *H. larutensis*, *H. margarethae*, *H. titiwangsaensis* n. sp., and *H. yunnanensis*. Potentially unique bisexual populations occur in Hong Kong, southern Indochina, Borneo, and Sri Lanka, but samples are too small to adequately characterize these populations. The origins and evolution of the species are examined, and the study concludes with a taxonomy for the identified species.

Cover image: Palauan slender gecko *Hemiphyllodactylus ganoklonis*. (Drawing by Molly Dwyer Griffin.)

Dedication

I dedicate this taxonomic study to Jay M. Savage
for the excellence of his half-century of biogeographic
and systematic research and in appreciation for his
professional support—often "behind the scenes"—and
friendship throughout my herpetological career.

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Preface

My fascination with *Hemiphyllodactylus* began during a study of Fijian lizards. Often, the presence or absence of secreting precloacal and/or femoral pores is used to determine the sex of adult geckos: males possess them, females do not. Although a reliable assumption for some gekkonid and iguanid lizards, a chance observation on an adult Fijian *Hemiphyllodactylus typus* showed its potential for incorrect sex determination. The Fijian specimen had well-developed pores, yet I remained uncertain of sex even though its gonads appeared to be ovaries. Histology of a gonad revealed developing follicles, thus the specimen was an adult female. Other adult *H. typus* from Oceania had pores, and examination of their gonads revealed that all were females. This evidence suggested that all Pacific *H. typus* populations are unisexual (Zug, 1991). Further, this discovery caused me to continue my examination of *Hemiphyllodactylus* specimens and led to an observation that all individuals from coastal localities from Hawaii and Tahiti westward to New Guinea and those of the Mascarenes share the *typus* morphotype and are females.

Not all *Hemiphyllodactylus* populations, however, are unisexual. The bisexual populations typically occur inland in forested situations from Palau and the Philippines to Sri Lanka and the Eastern Ghats of India. There are a variety of names available for these populations (Kluge, 2001): *insularis*, *harterti*, *yunnanensis*, *aurantiacus* (east to west); and other available names not listed by Kluge. My primary goal here is to examine morphological variation among all populations of *Hemiphyllodactylus* and to address the systematics issues that arise from this study.

Speciation and Dispersal in a Low Diversity Taxon: The Slender Geckos *Hemiphyllodactylus* (Reptilia, Gekkonidae)

George R. Zug, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC 162, Washington, D.C. 20013-7012, USA; zugg@si.edu. Manuscript received 31 August 2009; accepted 5 May 2010.

INTRODUCTION

Hemiphyllodactylus are small, inconspicuous geckos but incredibly wide-ranging in the Indo-Pacific realm. The *H. typus* morphotype occurs from the Mascarenes eastward through southern Asia to eastern Polynesia and Hawaii. Throughout this broad distribution, these geckos are not commonly seen, even by biologists looking for them; thus they have attracted little attention by herpetologists and hobbyists.

How does such an inconspicuous gecko attain such a broad occurrence? Human transportation seems the obvious answer, although the subsequent questions of how, why, and when are largely unanswered. The search for a data-supported answer is one of the goals of this study. The major goal is to uncover the diversity of this taxon and to place this diversity in a firm taxonomic setting.

Nomenclatural History

Bleeker (1860) was the first naturalist to recognize the uniqueness of this small gecko. He described his Sumatran gecko as a new species and genus. His description is adequate, and the survival of the type specimen assures that *Hemiphyllodactylus typus* Bleeker is associated correctly with a gecko population today. Although the assignment of the name to a specific taxon is unambiguous, confusion exists about the type locality and the nomenclatural status of *Ptyodactylus gracilis*. These difficulties arise from the last sentence in Bleeker's description (1860:237): "Ik bezit eene afbeelding dezer soort; afkomstig van de voormalige Natuurkundige kommissie, voorzien van den naam *Ptyodactylus gracilis* en naast welke aangeteekend is, dat de soort ook op den Goenong Parong (Java) leeft." My interpretation (based on a translation by T. Ulber, in litt.) is that Bleeker is telling the reader that the yellow underside of the tail

and other characteristics (from the preceding descriptive sentence) are seen in an illustration of his new species that is labeled *P. gracilis*; the source of this illustration is presumably an unpublished report of the Natuurkundig Commission. As interpreted by Wermuth (1965) in his gekkonid checklist, Bleeker was not offering a substitute name. Kluge (1968:342) noted this error of interpretation, and he proposed correctly that "a picture (drawing) of his [Bleeker's] new species . . . bore the name *Ptyodactylus gracilis*." Ulber's translation shows that Bleeker was noting that *H. typus* also occurred at Goenong Parong (Java) based on an unpublished illustration. *Ptyodactylus gracilis* is thus a nomen nudum and unavailable.

Kluge (1968:342) noted that the association of Goenong Parong with *P. gracilis* "led Smith (1935) and Wermuth (1965) to incorrectly consider the type locality of *typus* as Goenong Parong, Java." Kluge's identification of the type locality (Figure 1) with the title of Bleeker's article is correct, that is, Agam, a locality in central Sumatra (see gazetteer in David and Vogel, 1996).

Bleeker was not the only naturalist to recognize the uniqueness of this gecko. Bavay discovered this gecko on buildings during his field work in New Caledonia. He recognized it as a new species, *Platydactylus crepuscularis*, in his catalog of New Caledonian reptiles (Bavay, 1869), apparently unaware of Bleeker's description. While he noted this gecko's similarity to *Lepidodactylus lugubris*, at least to the description of that taxon provided by Duméril and Bibron, Bavay's description explicitly characterized *P. crepuscularis* as a *Hemiphyllodactylus typus* Bleeker; thus *P. crepuscularis* is a junior subjective synonym. The history of this name and its type specimens is detailed in Bauer's (1994) comment sections for *H. typus* and *L. lugubris*. I wish to examine only one aspect—the holotype or syntypes of *P. crepuscularis*. Bavay typically gave the dimension of a single specimen in his species accounts, whether describing a new or established taxon. Boulenger (1883:123), however, suggested Bavay had two specimens: "and two others, male and young, the types of the species, communicated to me by M. Bavay." Was the "communicated" a letter with data on the specimens or actual specimens sent to Boulenger? If the latter, they were not cataloged in the British Museum, because Boulenger (1885) listed only the two Benchley specimens that he had mentioned in his 1883 description. There is no evidence that Bavay deposited the type(s) in the Paris Museum, because Sauvage's (1879) subsequent description of a type was based on a specimen of *L. lugubris* (see Bauer, 1994). Hence the type of *P. crepuscularis* is lost, but fortunately Bavay's description clearly refers to *H. typus* Bleeker.

Major Beddome, a forestry officer in Madras (present-day Chennai, India), collected a variety of reptiles and described them in 1870. One of them, *Hemidactylus aurantiacus* Beddome, was a *Hemiphyllodactylus* species from mid-elevation in the Shevaroy Hills. Nothing in Beddome's characterization identifies the new species unequivocally as *Hemiphyllodactylus*. Boulenger's (1885) description is more detailed, and his placement with *Lepidodactylus* was a better assessment of *aurantiacus'* affinities. Boulenger also noted that the type series consisted of many adult males, females, and juveniles.

Günther (1872) described a *typus* gecko from the "East-Indian archipelago" as *Spathodactylus mutilatus*. The generic and specific descriptions and the illustration of the fore- and hindfeet readily identify the holotype as *Hemiphyllodactylus* and likely *H. typus*. Although Günther did not identify the source of the specimen, Boulenger (1885) did—Dr. Bleeker. This information suggests that the types of *H. typus* Bleeker and *S. mutilatus* Günther are the same specimen; thus the latter name is a junior objective synonym of the former. Because Boulenger included neither *Hemiphyllodactylus* nor *typus* as names in his catalog, it indicates that neither he nor Günther was aware of Bleeker's description. Boulenger (1885) did recognize that Günther's *Spathodactylus* was a homonym for a fish and provided a new generic name *Spathoscalabotes*. Subsequently, Malcolm Smith (1935) listed the type locality of *S. mutilatus* as Agam, Sumatra, in his synonymy of *H. typus*; this restriction is correct owing to Bleeker's original source of the specimen, although in the same synonymy, Smith incorrectly gave Java as the type locality of *H. typus* Bleeker.

As noted above, Boulenger (1885) was apparently unaware of Bleeker's description of *Hemiphyllodactylus* and *H. typus*, because these names are absent from his catalog. He placed *crepuscularis*, *ceylonensis*, and *aurantiacus* in the genus *Lepidodactylus* and continued to recognize Günther's *mutilatus* as a monotypic taxon although correcting the generic homonymy.

Boulenger followed the species account of *Lepidodactylus crepuscularis* (=*Platydactylus crepuscularis* Bavay) with an exceedingly brief description of *Lepidodactylus ceylonensis*. The description identifies the specimen as *Hemiphyllodactylus* only by Boulenger's (1885:164) statement: "This species resembles exactly the preceding [*L. crepuscularis*] in proportions, pholidosis, and coloration." Boulenger's illustration is suggestive of *Hemiphyllodactylus,* but it would fit other geckos as well.

Stejneger (1899) provided the first review of the Hawaiian terrestrial reptiles. Of the seven lizard species then
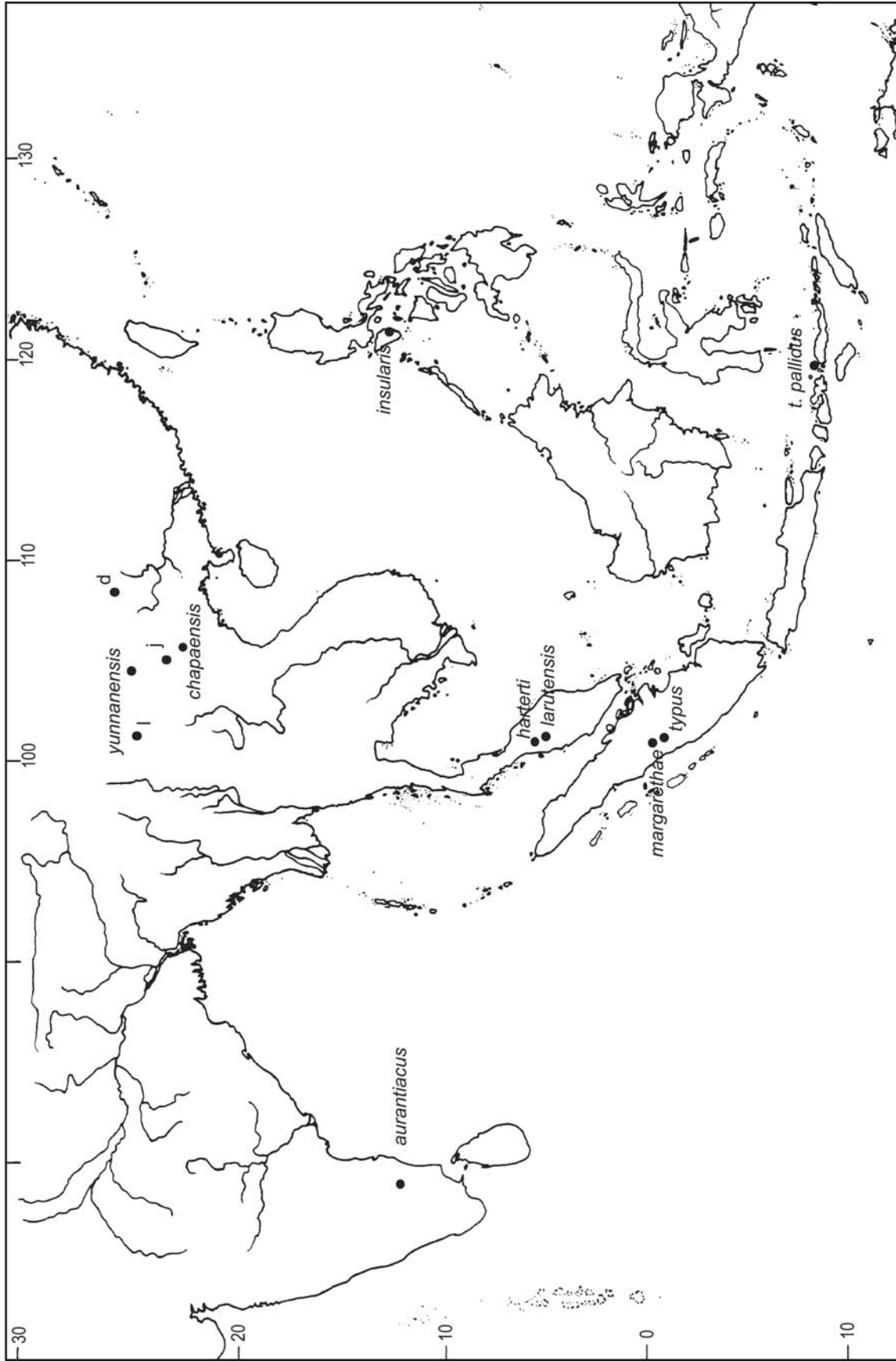
FIGURE 1. Type localities for the available names (see Table 1) for the species currently assigned to genus *Hemiphyllodactylus*. Abbreviations: d, *H. yunnanensis dushanensis*; j, *H. y. jinpingensis*; l, *H. y. longlingensis*.

occurring on these islands, only one appeared to represent a new species, *Hemiphyllodactylus leucostictus* Stejneger. Stejneger gave a thorough description and included illustrations of the head, pelvic area, and hindfoot of his new species. He stated that the differences of the Hawaiian specimens to *H. crepuscularis*, *H. ceylonensis*, and *H. typus* were slight but real, hence appropriate to recognize a new species.

Werner (1900) received a single small gecko from Malakka (now Malaysia) and noted its distinctiveness. He named it *Lepidodactylus Harterti* after the collector and ornithologist Ernest Johann Otto Hartert. He highlighted the presence of strongly V-shaped lamellae (11 on fourth toe) and proposed that it was closely related to *Lepidodactylus lugubris*, although the inner digit was less well developed than in *L. lugubris*.

Boulenger examined a small collection of amphibians and reptiles from the Larut Hills, Perak, Malaysia, many of which were new. His descriptions (Boulenger, 1900) of the new species included a new gecko, *Gehyra larutensis*. It is unclear why he had shifted his generic placement of *typus*-like geckos. Using the same generic assignment three years later, Boulenger (1903) described another *typus*-like gecko from China, *Gehyra yunnanensis*. In both descriptions, he mentioned the low number of chevron-like lamellae on the digits characteristic of *Hemiphyllodactylus* geckos. He continued to use *Gehyra* for these geckos in his book on the Malayan herpetofauna (Boulenger, 1912). More importantly, Boulenger (1912:48) noted that *G. larutensis* "may prove to be identical with this species [*H. harterti* Werner, 1900]." He further noted that Werner's Malakka type locality should be replaced by Gunong Inas, a site where Hartert collected birds in 1888 (Hartert, 1901, 1902). The nomenclatural significance of this tentative correction [reassignment] is addressed in the Taxonomic Decisions and Geography section.

In *Reptiles of the Indo-Australian Archipelago*, de Rooij (1915) recognized *Hemiphyllodactylus typus* and *Lepidodactylus ceylonensis*. She used the digital lamellar morphology and rudimentary and clawless first digits as the main diagnostic features for *Hemiphyllodactylus*. De Rooij was the first researcher to recognize a broad distribution for *H. typus* and reported its occurrence widely in Sumatra and Java and on Borneo. She used *Lepidodactylus ceylonensis* as an all-encompassing taxon defined by a rudimentary first finger and with a distribution from Borneo through Java, Sumatra, and Nicobar to Myanmar and Sri Lanka.

Taylor (1918) recognized that the Philippine *typus* gecko as *Hemiphyllodactylus insularis*. He compared it only to *H. leucostictus* Stejneger, noting that he was uncertain that the Hawaiian gecko was "actually distinct."

Presumably, he meant distinct from *H. typus*; however, he does not mention Bleeker's taxon or any of the other *typus*-like taxa. Taylor was the first systematist to discuss variation within a type series (Mindoro) of a *typus*-like taxon as well as presenting geographic variation of specimens from other islands in the Philippines. He was also the first author to provide natural history observations, noting that females lay two adhesive eggs beneath tree bark and that all specimens were beneath bark on seaside trees.

In 1924, Barbour received specimens of *Hemiphyllodactylus yunnanensis* from The Reverend John Graham, who had provided the original series of specimens to Boulenger. Barbour was so struck by the morphology of foot lamellae that he proposed a new generic name for this taxon, *Cainodactylus*. Barbour stated that Dr. Stejneger agreed with him on the uniqueness of the foot morphology, but Barbour seemingly was so focused on the differences of his specimens to species of *Gehyra* and *Hemidactylus* that he overlooked Stejneger's description and illustrations of *H. leucostictus* and consequently created a synonym.

Brongersma (1931) described *Hemiphyllodactylus margarethae* from four Sumatran specimens representing two montane localities. He recognized this species' affinity and differentiated it from *H. typus* and *H. ceylonensis*. Subsequently, Brongersma (1932) published an evaluation of the nomenclature and characterization of *Hemiphyllodactylus* and its species. He recognized only two species: *H. aurantiacus* and *H. typus*. Although he recognized *H. aurantiacus*, Brongersma examined only two specimens and purposefully kept his remarks brief. Thus his "Notes" refer mainly to *H. typus*, in which he synonymizes *H. ceylonensis*, *H. crepuscularis*, *H. leucostictus*, *H. insularis*, and *H. margarethae*. He noted that M. A. Smith had independently reached the same conclusions. Brongersma reached his conclusion through the evaluation of three characters regularly used to diagnose *Hemiphyllodactylus* species: (1) denticulate digits, (2) number of precloacal pores, and (3) if present, number of femoral pores. He concluded that denticulation was slight in most specimens and "purely individual" (Brongersma, 1932:214). He recognized the difficulty of distinguishing pits and pores, noted the absence of femoral pores in some males, and concluded that the number of pores (precloacal and femoral) "seems to be of no value in this genus" (Brongersma, 1932:216).

M. A. Smith's conclusions, revealed to Brongersma in a letter, were subsequently promulgated in his work on the lizards of British India (Smith, 1935). Therein, Smith recognized two species of *Hemiphyllodactylus*: *H. typus typus*, *H. typus aurantiacus*; and *H. yunnanensis*. The

nominate subspecies included as synonyms all the species mentioned in the preceding paragraphs except *H. laruten-sis*, thereby giving *H. typus* a distribution from Sri Lanka eastward into Oceania. *Hemiphyllodactylus t. aurantiacus* retained a southern India distribution. *Hemiphyllodactylus yunnanensis* was identified with a Yunnan, northern Laos, and northern Myanmar distribution. In a footnote, Smith (1935:109) proposed that *H. yunnanensis* was "perhaps a northern representative of the Malayan *Hemiphyllodacty-lus larutensis* (Boulenger)." Smith (1933) in an article that likely was preparatory to his 1935 catalog examined the confusion of species assignment to *Hemiphyllodactylus*. Therein he provided a concise definition of the genus and a list of three included species: *typus*, *yunnanensis*, and *harterti*. He noted that the latter name had appeared three months before *Gehyra larutensis* Boulenger.

Bourret (1937) described *Hemiphyllodactylus typus chapaensis* from northern Vietnam (Chapa, Tongking). He noted that it resembled *H. yunnanensis* but that his taxon was not greatly different from *H. typus*, hence his assignment to subspecific status. His description included five detailed illustrations of the type.

After Bourret, *Hemiphyllodactylus* occurred irregularly in the herpetological literature until the 1960s, typically in regional lists, reappearing in Taylor's lizards of Thailand (Taylor, 1963) with a full description and Wermuth's (1965) checklist of all gekkonid lizards. Wermuth recognized three species (*larutensis*, *typus*, and *yunnanensis*) and three subspecies of *H. typus* (nominate form, *aurantiacus*, and *chapaensis*). Kluge (1968) addressed the relationships of *Hemiphyllodactylus* as well as commenting on nomenclatural matters; these matters were discussed above. He considered *typus* and *yunnanensis* as full species of *Hemiphyllodactylus* and left the status of *aurantiacus*, *chapaensis*, and *harterti* for additional investigation. Kluge considered *Hemiphyllodactylus* as a sister group of *Lepidodactylus*. This hypothesis returns conceptually to Boulenger's catalog treatment, although retaining *typus* and its congeners as a separate genus (lineage).

Wermuth (1966) reexamined a gecko, *Platydactylus minutus* Giebel 1862, captured in Baltic amber. He proposed that the specimen was a *Hemiphyllodactylus typus*. His Figure 2 of the right forefoot shows subdigital lamellae similar to those of *H. typus*; however, the dorsal view of the entire gecko (Wermuth, 1966: fig. 1) is not *typus*-like. The head, neck, and body are robust and not elongated. The fore- and hindlimbs are large, long, and would overlap one another if laid along the trunk. With this habitus, *Platydactylus minutus* Giebel is not a synonym of *H. typus* or vice versa.

Through the 1970s and 1980s, *Hemiphyllodactylus* species, mostly *H. typus*, appeared in assorted publications on regional herpetofaunas. For example, Brown and Alcala (1978) continued the interpretation of *H. insularis* as a synonym of *H. typus* in their Philippine gecko catalog. Auffenberg (1980) reviewed the herpetofauna of Komodo and observed that the Komodo *H. typus* were lightly colored and nearly patternless. He described the Komodo population as the subspecies *H. t. pallidus*. Zhou et al. (1981) examined a large collection of *H. yunnanensis* from Yunnan, Guizhou, and Guangxi Provinces, China, and observed regional variation in digital lamellae patterns. Because the variation was concordant within four regions, they recognized three new subspecies: *H. y. du-shanensis*, *H. y. jinpingensis*, and *H. y. longlingensis*.

Lazell (1989) made an unexplained alteration (1989) of *leucostictus* Stejneger to *albostictus* in a magazine article. Zug (1991) revealed the unisexual aspect of Fijian and other Oceania populations of *H. typus*. Bauer's (1994) checklist of Australian and Oceania gekkonids provided a full synonymy of *Hemiphyllodactylus typus* and an abbreviated review of the various nomenclatural usage and alterations. Manthey and Grossmann (1997) recognized two species (*larutensis*, *typus*) of *Hemiphyllodactylus* in the Sunda area. The two have strikingly different coloration in their illustrations and descriptions, confirming the presence of two species in this area. Their concept of *H. typus*, however, was as a bisexual species, with males defined by the presence of femoral–precloacal pores. Soon thereafter, Chan-ard et al. (1999) listed four species (*harterti*, *larutensis*, *typus*, and *yunnanensis*) from Thailand and peninsular Malaysia. Their photographs show variable coloration among the specimens identified as *H. harterti* and *H. larutensis* from the Cameron Highlands, Pahang State, Malaysia.

Subsequently, Bauer and Das (1999) visited the type locality of *Hemidactylus aurantiacus* Beddome and captured three adult specimens. Their examination of these specimens and specimens from Malaysia, Philippines, and elsewhere demonstrated that the Shevaroyan geckos had several diagnostic traits that clearly distinguished this midmontane population from other *Hemiphyllodactylus typus*. On the basis of these consistent differences, they recognized *Hemiphyllodactylus aurantiacus* as a full species. Kluge's most recent gekkonid checklist (Kluge, 2001) similarly returned *Hemiphyllodactylus insularis* Taylor to specific status but without explanation. Gaulke (2003) briefly examined the nomenclatural history of Philippine *Hemiphyllodactylus* and, presumably because of the presence of males and females, accepted *H. insularis* as a distinct taxon from *H. typus*. The available names for the

TABLE 1. Available names for populations and species of *Hemiphyllodactylus* geckos. Type localities presented are from the original descriptions; because many of these localities may not be obvious or known to some readers, the country in which the locality occurs is included in brackets.

Date	Name	Author	Type locality
1860	*Hemiphyllodactylus typus*	Bleeker	Agam [Sumatra]
1869	*Platydactylus crepuscularis*	Bavay	Nouvelle-Calédonia
1870	*Hemidactylus aurantiacus*	Beddome	Shevaroys . . . about Yercaud [India]
1872	*Spathodactylus mutilatus*	Günther	East Indies archipelago
1885	*Lepidodactylus ceylonensis*	Boulenger	Ceylon
1899	*Hemiphyllodactylus leucostictus*	Stejneger	Kauai, Hawaiian Islands
1900	*Lepidodactylus Harterti*[1]	Werner	Malakka [Malaysia]
1900	*Gehyra larutensis*	Boulenger	Larut Hills [Malaysia]
1903	*Gehyra yunnanensis*	Boulenger	Yunnan Fu [China]
1918	*Hemiphyllodactylus insularis*	Taylor	Sumagui, Mindoro [Philippine Islands]
1931	*Hemiphyllodactylus margarethae*	Brongserma	Fort de Kock, Sumatra
1937	*Hemiphyllodactylus typus chapaensis*	Bourret	Chapa [Vietnam]
1980	*Hemiphyllodactylus typus pallidus*	Auffenberg	Vai Nggulung, Loho Liang, Komodo
1981	*Hemiphyllodactylus yunnanensis dushanensis*	Zhou et al.	Dushan County, Guizhou Province, China[2]
1981	*Hemiphyllodactylus yunnanensis jinpingensis*	Zhou et al.	Jinping County, Yunnan Province, China[2]
1981	*Hemiphyllodactylus yunnanensis longlingensis*	Zhou et al.	Longling County, Yunnan Province, China[2]

[1] *Harterti* is capitalized as it appears in the original description.
[2] Type locality presented in Chinese.

various populations of *Hemiphyllodactylus* are summarized chronologically in Table 1.

MATERIALS AND METHODS

Despite the broad distribution of *Hemiphyllodactylus*, the availability of voucher material in museum collections is relatively poor. The assembly of an adequate quantity of specimens required access to many collections; the collection names 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
CAS	California Academy of Sciences
CM	Carnegie Museum of Natural History
FMNH	Field Museum of Natural History
IRSNB	Institut royal des Sciences naturelles de Belgique
KUZ	Kyoto University, Department of Zoology
MCZ	Museum of Comparative Zoology, Harvard University
NMB	Naturhistorisches Museum, Basal
NMW	Naturhistorisches Museum, Wien
QM	Queensland Museum
RMNH	Nationaal Natuurhistorisch Museum (formerly Rijkmuseum van Natuurlijke Historie)
SAM	South Australian Museum
SDMNH	San Diego Museum of Natural History
SMF	Natur-Museum u. Forschungs Institut Senckenberg
THNHM	Thailand Museum of Natural History, National Science Museums
UF	Florida Museum of Natural History, University of Florida
USNM	U.S. National Museum (National Museum of Natural History, Smithsonian Institution)
WAM	Western Australian Museum
WmBeckon	William N. Beckon, private collection
ZMA	Zoölogische Museum, Universiteit van Amsterdam

ZMB	Museum für Naturkunde, Universität zu Humboldt
ZMFK	Zoologische Forschungsinstitut u. Museum Alexander Koening
ZRC	Zoological Reference Collection, National University Singapore
ZSM	Zoologisches Sammlung des Bayerischen Staates

I grouped the specimens into 13 regional samples, each representing a putative biogeographic area abbreviated in small capitals and defined as follows:

CHINA	China and northeastern Myanmar
FIJI	Fiji and Tonga
HAWAI	Hawaiian Islands
INDIA	India and Sri Lanka
MASCAR	Mascarenes
NCAL	New Caledonia and Vanuatu
NGUIN	New Guinea and Solomon Islands
PALAU	Republic of Palau
PHILIP	Philippine Islands
POLYN	Polynesia
SEASIA	Thailand (north of Isthmus of Kra) to Vietnam and Hong Kong
SUNDA	Malaysia and Indonesia
TAIWAN	Taiwan and Japan

These regional samples vary in size (n = 9–85) and geographic extent. In the latter case, a sample can be examined as two or more subsamples of restricted localities if adequate specimens are available or if intrasample variation indicates a mixed sample. Further, I combined samples and repartitioned specimens when an initial analysis suggested the presence of multiple bisexual taxa in one or more of geographically adjacent samples.

Morphological data consist of a combination of morphometric and meristic characters. These characters are identified and their abbreviations defined in Appendix 1. Sex and maturity were determined by dissection and examination of the gonads. Maturity criteria were those outlined in Zug et al. (2003). The small size of this taxon seems to have resulted in a high level of inattentiveness to the preservation and positioning of specimens. Contorted specimens, commonly with clenched fore- and hindfeet, made data-gathering challenging and certainly increased the variation in most measurements and scale counts.

The data were analyzed by a variety of univariate and multivariate statistics using SYSAT version 11. My goal has been to examine and describe intra- and interpopulational variation as thoroughly as possible considering the variable preservation state of many specimens. The multivariate models were used as exploratory techniques to compare populations and possibly reveal differentiation within and among samples. Explanation of the use of the multivariate analyses and the results are available in Appendix 3.

In addition to the abbreviations defined above and in Appendix 1, other symbols and abbreviations used in this publication are defined as follows:

alt.	altitude
CV	coefficient of variation
DFA	discriminant function analysis
GPD	glycerosphophate dehydrogenase
IDH	isocitrate dehydrogenase
MPI	mannose phosphate isomerase
PCA	principal components analysis
SD	standard deviation
r^2	coefficient of determination

CHARACTER ANALYSIS: RESULTS AND DISCUSSION

BASELINE ESTIMATE OF INTRA-OBSERVER VARIATION

How much of the variation observed in each sample results from the researcher's data-gathering behavior? Hayek et al. (2001) addressed that question and recommended a repeated measuring protocol to obtain an estimate of this portion of a character's and a sample's variation. A single specimen (in this case USNM 563683, female from Palau) was measured and scalation recorded 10 times, each time on a separate day over a period of 6 weeks. Central tendency statistics reveal that for measurements, the coefficients of variation (CVs) range from 0.7% (mean snout–vent length [SVL] = 32.5 mm ± SD 0.24) to 9.3% (mean SnW = 1.1 mm ± SD 0.10). The larger measurements (SVL, TrunkL, HeadL, HeadW—see Appendix 1 for definitions) have the least variation (CV, 0.7–1.9%) relative to the smaller ones (SnEye, NarEye, EyeD, SnW; CV, 3.2–9.3%). The coloration traits were invariant, as were the majority of the scalation characters. Ventral (mean = 9.3 mm ± SD 1.16) and 2ToeLm (3.7 mm ± SD 0.48) had the highest CVs (12.5%, 13.1%, respectively); in all other variable traits, CV was <8%.

These results provide a baseline for assessing the variation observed in regional samples. Further, these estimates probably represent the lowest variation for the *Hemiphyllodactylus* data as they were recorded from a well-preserved and well-positioned specimen and collected under optimal laboratory conditions. While the data

reported throughout this study were gathered by a single individual (me), they were gathered over two decades (1989–2008) and in a variety of museum situations. As noted above, *Hemiphyllodactylus* specimens infrequently receive adequate preparation attention when collected. In spite of the inattentive preparations, the subsequent results reveal that intrasample variation is surprisingly low in most characters and samples; nonetheless, the reader is advised to be cautious in over-interpreting reported differences, particularly in small samples and/or where differences are less than 2 times a character's standard deviation.

RECOGNITION OF UNISEXUAL AND BISEXUAL POPULATIONS

Unisexual populations contain only females. Although it may be a statement of the obvious, how does one confirm the unisexuality of a population? Because neither data on reproduction of virgin females nor mitochondrial DNA were available to me, I relied on the absence of males in samples as a hypothesis of unisexuality for populations or sets of populations. On that basis, the Hawaiian (HAWAI), Polynesian (POLYN), Fijian–Tongan (FIJI), New Caledonian–Vanuatuan (NCAL), New Guinean–Solomons (NGUIN), Taiwan (TAIWAN), and Mascarene (MASCAR) samples are considered unisexual populations. All other samples contain males, but owing to their manner of assembly, some samples, especially the Sundaland (SUNDA) and Indian–Sri Lankan (INDIA) ones, are likely mixtures of unisexual and bisexual individuals.

This situation requires an assumption: *Hemiphyllodactylus typus* Bleeker (BMNH 1946.8.30.83) represents (is) a unisexual species. The holotype is an adult female with precloacal and femoral pore series separated. To test this assumption, the initial character analyses examined variation in and among the Pacific samples (HAWAI, POLYN, FIJI, NCAL, NGUIN, TAIWAN) and then when they proved geographically homogeneous compared them to the type specimen. Assuming that this comparison yielded accurate "diagnostic" data, *H. typus* specimens were removed from the mixed unisexual–bisexual samples prior to examination of bisexual's within sample and between (interregional) sample variation.

Unisexual—Visceral Anatomy

Because sex and maturity were determined by dissection, I observed a consistent pattern of differential pigmentation in the viscera of Pacific *Hemiphyllodactylus*, although I did not report this observation in my study of Fijian lizards (Zug, 1991). All Pacific specimens have the caecum and oviducts heavily pigmented (melanin) (Figure 2A,B). For

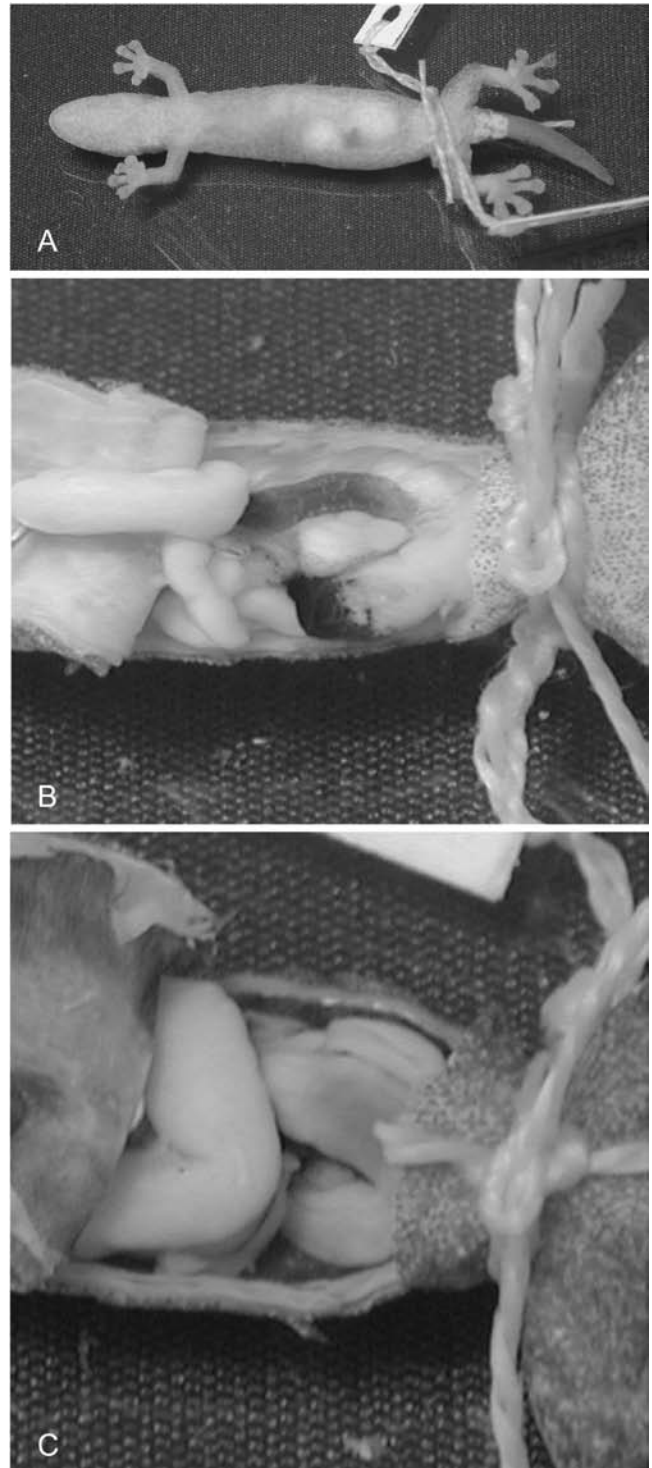**FIGURE 2.** Visceral pigmentation of *Hemiphyllodactylus* species. All images in ventral view. (A) Pigmented caecum visible externally between pair of oviducal eggs, *H. typus,* Hawaii (U.S. National Museum [USNM] 570747); (B) pigmented caecum and oviduct, large intestine inflected anteriorly (left side of image), *H. typus,* Hawaii (USNM 570742); (C) unpigmented caecum and oviduct, *H. yunnanensis*, Myanmar (USNM 570734).

the oviduct the peritoneum sheath likely bears the melanin. The pigmented caecum and oviducts, however, are not confined to the unisexual samples. This pigmentation pattern is widespread, but not global, in bisexual samples.

The black caecum is often visible through the ventral body wall and skin (Figure 2A). The pigmentation of the oviducts is darkest in virgin females. It is invisible in the greatly stretched oviducts of gravid females. The oviducts become dusky brown once the eggs are expelled. The duct walls retain a flaccid and stretched morphology following the first egg production cycle.

The type of *Hemiphyllodactylus typus* Bleeker was not dissected, so I am unable to confirm the pigmentation of its oviduct or its sex by a direct examination of the reproductive tract. It does not show any thickness at the base of the tail, thereby indicating the absence of hemipenes. The black caecum is visible through the body wall.

PRÉCIS. Unisexual *Hemiphyllodactylus typus* possess darkly pigmented caeca and oviducts. Bisexual *Hemiphyllodactylus* are variable in this pair of traits.

Unisexual—Morphometry

HAWAI is the largest of the Pacific samples and serves as a base to examine levels of variation and differentiation within and among the Pacific samples. HAWAI has neither the largest nor smallest adult females. Its mean and median SVL (36.7 and 36.3 mm) match those of POLYN and TAIWAN and is less than those of the other samples. NGUIN and FIJI are similar, with mean/median of 40 mm SVL. The smallest adult (29.2 mm SVL) is from TAIWAN; the largest (46.1 mm) is from FIJI. The other eight mensural traits show the same pattern of similarity among the samples. Intrasample variance is also similar within and among the Pacific samples, as seen by a comparison of the ranges of the coefficient of variation (CV) with the CV for the HAWAI datum: SVL 6.5% (HAWAI datum), 3.0–10.4% (range for the Pacific samples); TrunkL 11.3%, 5.2–11.7%; HeadL 5.0%, 4.6–8.3%; SnEye, 7.0%, 5.0–13.9%; NarEye 7.9%, 6.9–12.8%; EyeD 7.2%, 6.5–11.3%; SnW 10.5%, 5.9–15.5%; HeadW 9.2%, 5.1–12.1%. The higher CVs are associated mainly with TAIWAN (n = 9), which has the greatest range of adult SVL (29.2–43.6 mm). MASCAR is also an all-female sample and presumably represents a unisexual population. Its CVs match those of the Pacific samples (Table 2). Variation and means of the samples, either individually or combined (i.e., total Pacific unisexual sample; PACIF), are equivalent. There is no evidence of mensural differentiation among the Pacific insular samples or the distant MASCAR sample. Principal components analysis (PCA) and discriminant function analysis (DFA)

of the combined Pacific samples, MASCAR sample, and the holotype of *H. typus* similarly reveal a uniform morphology among these geckos. (See synopsis of PCA and DFA results in Appendix 3.)

The Pacific unisexuals and *typus* holotype are slender, elongate geckos (Figure 3). The proportionately short limbs accentuate the trunk elongation. A proportion of hindlimb length to trunk length would demonstrate this morphology; however, my preliminary measurements of hindlimb length were extremely variable owing to the difficulty of measuring accurately tiny twisted limbs with fist-like preserved feet in many specimens. Thus I excluded this trait from subsequent data gathering. The proportion TrunkL/SVL provides a metric, although a less satisfactory one, for portraying the relative elongation of the trunk. Linear regression of the two preceding traits also reveals the degree of elongation through the depression of the slope; however, in contrast to the proportion, variation from linearity (as measured by coefficient of determination, r^2) was high, thereby reducing the reliability of the slope as indicator of trunk elongation. The means and standard deviations for TrunkL/SVL (as percentage) among the Pacific *typus* samples are 52.0% ± 4.0 (HAWAI), 54.4% ± 3.5 (POLYN), 55.4% ± 4.2 (FIJI), 52.6% ± 1.6 (NCAL), 54.0% ± 2.4 (NGUIN), 52.9% ± 3.9 (PACIF). To place these proportions in the context of other geckos, the mean ± SD TrunkL/SVL for *Gehyra oceanica* is 42.7% ± 3.3 (n = 113), *Hemidactylus frenatus* is 42.0% ± 2.8 (n = 21), and *Lepidodactylus lugubris* is 44.1% ± 3.2 (n = 149). Trunk length is over 50% of total SVL in the *H. typus* samples and distinctly less than half of SVL in other Pacific geckos. Part of this proportional difference derives from a smaller head in *H. typus*, that is, 21.3% ± 0.9 HeadL/SVL (PACIF), as compared to 26.7% ± 1.6 for *G. oceanica*, 26.4% ± 1.6 for *H. frenatus*, and 24.2% ± 1.7 for *L. lugubris*. Combining the head and trunk proportions shows that neck length is proportionately shorter in *H. typus* in contrast to the visual impression of the attenuate habitus of *H. typus*.

Do these proportions permit the segregation of unisexual *H. typus* from bisexual *Hemiphyllodactylus*? Any of the regional samples might contain both unisexual and bisexual species. Because the SUNDA most certainly is mixed, it is the appropriate sample on which to test the morphometrics for differentiation.

The SUNDA sample (n = 83) contained 55 adult females of which 39 were identified as *H. typus* during data collection (based on coloration and pigmentation of caecum and oviducts), 15 males and 7 females as unknowns or uncertains, the holotypes each of *H. larutensis* (Boulenger) (adult male) and *H. harterti* (Werner) (adult female), holotype (adult male) and three paratypes (2 adult females,

TABLE 2. Summary statistics on select characters of unisexual *Hemiphyllodactylus* samples. Statistical values are mean (mensural traits) or median (scalation) ± standard deviation (SD), range of minimum to maximum, and coefficient of variation (CV); and modes and frequency (%) of occurrence (finger and toe lamellae). Sample sizes (*n*) are mature females and total sample, respectively; statistics derive solely from adults for mensural traits, and from juveniles and adults for scalation ones. The *n* value is the total number of specimens examined for each locality sample; the actual statistic may have derived from fewer individuals because not all characters could be measured or counted in all specimens. Character abbreviations are defined in Appendix 1.

Character and statistic	*typus* Holotype (1)	Hawaiian Islands (37, 42)	Total Pacific unisexual sample (99, 118)	Mascarene group (8, 11)
SVL				
Mean ± SD	43.3	36.7 ± 2.28	38.0 ± 2.91	38.1 ± 1.00
Range		32.4–42.8	29.2–46.1	38.1–40.9
CV		6.2%	7.6%	2.5%
TrunkL				
Mean ± SD	22.4	19.4 ± 1.94	20.2 ± 2.37	20.7 ± 1.31
Range		15.1–23.9	14.0–28.0	19.2–23.1
CV		10.0%	11.8%	6.3%
HeadL				
Mean ± SD	9.1	7.9 ± 0.38	8.1 ± 0.55	8.3 ± 0.26
Range		7.1–8.8	6.6–9.9	7.8–8.6
CV		4.8%	6.8%	3.2%
SnEye				
Mean ± SD	3.7	3.3 ± 0.22	3.3 ± 0.29	3.5 ± 0.16
Range		2.7–3.7	2.3–4.1	3.3–3.8
CV		6.8%	8.7%	3.5%
PostocSpt				
Median ± SD	[a]	4 ± 0.80	3 ± 0.95	3.2 ± 1.10
Range		1–5	1–5	2–5
CV		22.6%	29.7%	33.7%
SnS				
Median ± SD	3	2 ± 1.01	2 ± 0.81	2 ± 0.50
Range		1–5	1–5	2–3
CV		40.7%	37.7%	22.1%
Suplab				
Median ± SD	11	11 ± 0.85	11 ± 0.94	11 ± 0.82
Range		10–14	9–14	10–13
CV		7.6%	8.3%	7.3%
Chin				
Median ± SD	13	12 ± 0.99	11 ± 1.08	10 ± 0.71
Range		10–14	9–14	10–12
CV		8.4%	9.4%	6.7%
Dorsal				
Median ± SD	13	14 ± 1.53	15 ± 1.64	15.0 ± 1.48
Range		12–18	12–19	13–17
CV		10.6%	11.0%	10.0%
CloacS				
Median ± SD	2	3 ± 0.80	2 ± 0.79	2 ± 1.00
Range		1–5	0–5	1–4
CV		29.6%	34.0%	50.0%
4ToeLm				
Median ± SD	4	5 ± 0.33	5 ± 0.33	4 ± 0.47
Range		4–5	4–5	4–5
CV		6.8%	6.7%	8.4%
FingerLm [b]				
Modal values	3-3-4-3	3-4-4-4	3-4-4-4	3-4-4-3 [c]
Frequency		42.5%	47.7%	27.3%
ToeLm [b]				
Modal values	4-4-4-4	4-4-5-4	4-4-5-4	4-4-5-4
Frequency		51.2%	50%	36.4%

[a] This value/character is unknown in the holotype because of fading.
[b] Lamellae formulae represent the most frequent formula (mode) for each sample and the percent of the sample with this formula (frequency).
[c] Two finger formulae share 27%; the second is 3-4-4-4.
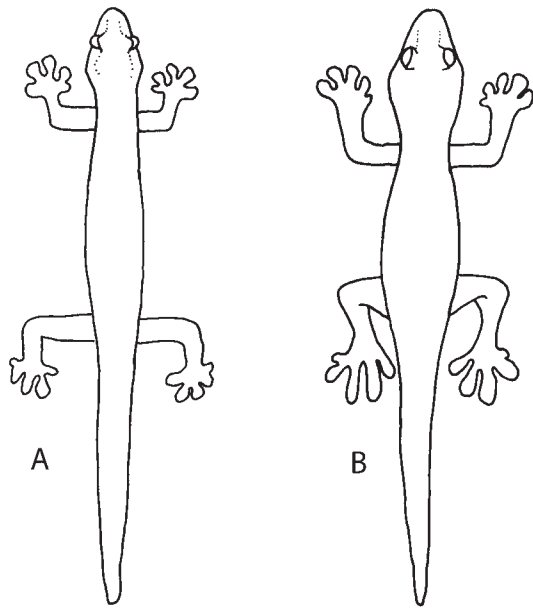
FIGURE 3. Contrasting habitus of adult *Hemiphyllodactylus*: (A) elongate morphotype, *H. typus*, Hawaii (USNM 27924); (B) robust morphotype, *H. yunnanensis*, China (British Museum of Natural History [BMNH] 1904.11.29.10D). (Illustration by J. Kilby.)

immature male) of *H. margarethae* Brongersma, and 11 (5 adult females, 6 adult males) other Malaysian "*harterti.*" The SUNDA *H. typus* included Bleeker's holotype. A PCA of the body proportions of all SUNDA females yielded a clustering of *H. typus* in the bottom quadrant of the PCA scores graph (Figure 4). EyeD/NarEye, NarEye/HeadL, and SnW/HeadW had the strongest loading (0.63–0.88) on the first component, HeadW/SVL and HeadL/SVL strongest loading (0.95, 0.81) on the second component, and SnW/HeadL and SnW/HeadW on third component (0.88, 0.66). The first three components accounted for 68% of the total variance (80%, with the inclusion of the fourth component). These results also place the *H. typus* holotype (BMNH 1946.8.3) within the *H. typus* cluster (Figure 4). The bisexuals lie principally outside the *typus* cluster in the upper left quadrant. One of the *H. margarethae* paratypes (ZMA 11096) is a distant outlier (upper right quadrant) from all other *Hemiphyllodactylus* females. The other *H. margarethae* paratype (IRNS9338B) is on the outer edge of the *typus* cluster. Overall, these results indicate a difference in head shape (PCA 1) and relative size (PCA 2) between the unisexual *H. typus* and the bisexual species. I note that I identified all Bornean females as *H. typus* and all Bornean males as unknown bisexuals. All Bornean females lie within the *typus* cluster. The holotype of *H. typus* (0.288, –1.362) lies within the lower half of the *H. typus* cluster (Figure 4B).
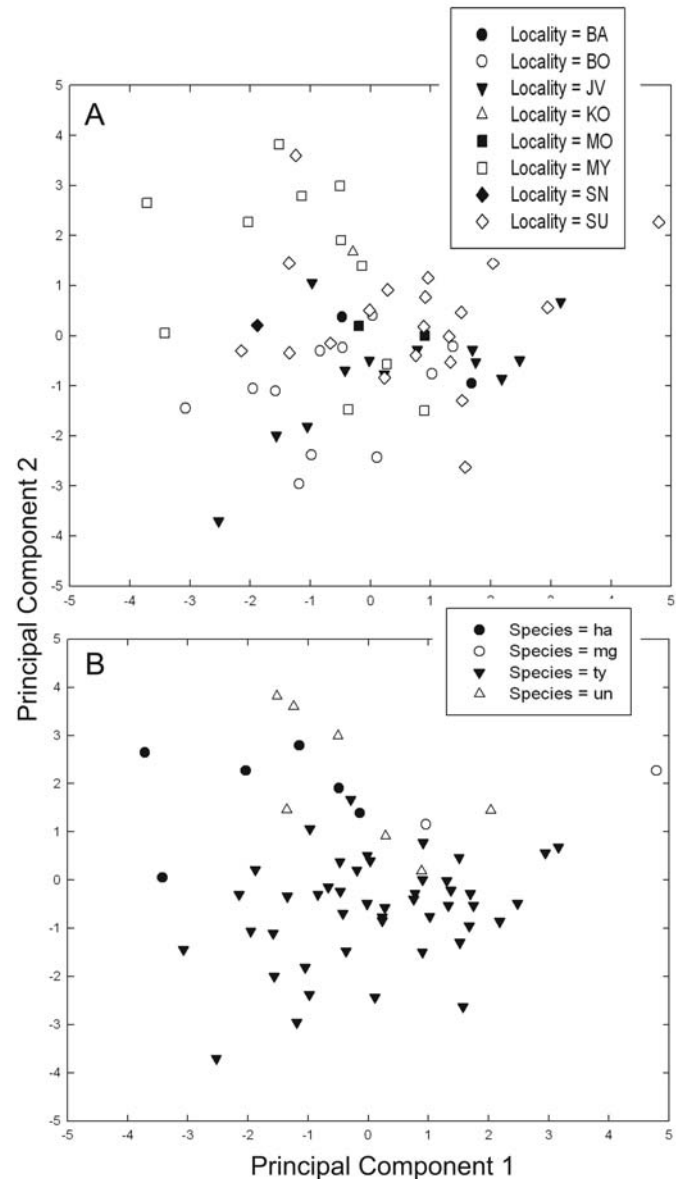
FIGURE 4. Distribution of unisexual and bisexual adult females of SUNDA *Hemiphyllodactylus* in multivariate (principal components) morphometric space: (A) Females identified by locality (LOC) and (B) females identified by species (ID). Abbreviation by locality: BA, Bali; BO, Borneo; JV, Java; KO, Komodo; MO, Mollucas; MY, Malaysia; SN, Singapore; SU, Sumatra. Abbreviations by species: ha (circle), *H. harterti*; mg (plus sign), *H. margarethae*; ty (square), *H. typus*; un (diamond), unknown/unassigned species.

The assignment of SUNDA specimens to *H. typus* was based on the presence of pigmented caeca and oviducts and, to a lesser extent, on dorsal coloration. The unknowns and bisexual type specimens had either unpigmented caeca or both oviducts and caeca unpigmented (Types were not dissected so oviducal pigmentation is usually unknown for

them.). Re-examining the proportions of the outliers and the types versus the *typus* specimens revealed that most (37 of 39 individuals) Sunda *H. typus* had mean TrunkL/SVL values ≥50% (52.3% ± SD 2.3, range of 46–56%) and a more ambiguous result in the other group. *H. margarethae* paratypes had TrunkL/SVL of 52% and 54%; the outliers were ≤50%, although not greatly so except for one Sumatran specimen (RMNH 7371, 40%). Sunda *H. typus* HeadL/SVL matched well the Pacif sample (mean 21.5% ± SD 1.0, range 19–23.8%), showing the small-headed condition; the bisexuals ranged 22.2–26.8%. The three highest loading proportions showed a greater degree of overlap between unisexuals and bisexuals, for example, EyeD/HeadL (highest loading on first component) 75.1% ± 8.6, 61–106% for unisexuals versus 49–81% for bisexuals; both the 49% and 106% values were extreme outliers of their samples and likely data collection errors.

The segregation of the unisexuals (*H. typus*) and bisexuals in the Sunda sample allowed a summary of the major statistics for the Sundan *H. typus* (*n* = 40, including the holotype): SVL (mean length ± SD, range): 38.7 mm ± 3.19, 32.3–44.1 mm; TrunkL: 20.3 mm ± 1.96, 16.9–24.2 mm; HeadL: 8.3 mm ± 0.62, 7.1–9.4 mm; TrunkL/SVL (mean proportion ± SD, range): 0.52 ± 0.02, 0.46–0.56; HeadL/SVL: 0.21 ± 0.01, 0.20–0.24; HeadW/HeadL: 0.65 ± 0.04, 0.55–0.63.

Philip is predominantly a bisexual sample, containing eight unisexuals from Palawan and two from Mindanao. The summary statistics of unisexuals are SVL: 39.0 mm ± SD 2.75 with range of 35.3–41.3 mm; TrunkL: 21.1 mm ± 1.84, 18.4–22.4 mm; HeadL: 8.3 mm ± 0.77, 7.2–9.0 mm; TrunkL/SVL (mean proportion ± SD, range): 0.54 ± 0.02, 0.52–0.57; HeadL/SVL: 0.21 ± 0.01, 0.20–0.22; HeadW/HeadL 0.70 ± 0.08, 0.66–0.82. The SEAsia sample includes only one unisexual (SVL 38.3 mm), confirmed by pigmented oviducts and caecum; this adult female, however, lacks secreting precloacal–femoral pores, thereby questioning its assignment to *H. typus*. India has four unisexual specimens but only in the Sri Lankan component of the sample; two other Sri Lankan specimens are bisexuals. One of the unisexuals is the holotype (BMNH 74.4.1326) of *Lepidodactylus ceylonensis* Boulenger. Summary statistics for the India *H. typus* are SVL (mean ± SD, range): 34.0 mm ± 10.43, 18.5–40.5 mm; TrunkL: 17.4 mm ± 5.34 9.4–20.5 mm; HeadL: 7.4 mm ± 1.98, 4.5–8.9 mm; TrunkL/SVL (mean proportion ± SD, range): 0.51 ± 0.02, 0.50–0.54; HeadL/SVL: 0.22 ± 0.02, 0.20–0.24; HeadW/HeadL: 0.66 ± 0.02, 0.63–0.67.

Précis. (1) The Oceania *H. typus* samples are homogeneous within and among samples, representing a single genetic entity and henceforth treated as a single sample (Pacif). (2) Morphometrics weakly differentiate unisexual individuals (*Hemiphyllodactylus typus*) from bisexual ones. Two proportions, TrunkL/SVL and HeadL/SVL, appear most useful in this differentiation.

Unisexual—Scalation

An overview of scalation variation within unambiguous unisexual samples is presented in Table 2. Intrasample variation, as estimated by CV, is nearly identical to intersample variation (i.e., CVs of Pacif), resulting from the similarity of means, medians, and ranges of the scalation traits; thus the subsequent character survey focuses on the Pacif sample and examines the regional samples only when one or more of the latter samples deviates from Pacif. As noted in the morphometric section, many museum vouchers were poorly positioned at time of preservation. Also, *Hemiphyllodactylus* are small geckos, and many were examined in circumstance of poor lighting and/or optics. I assumed that such circumstances would cause high variation, but fortunately, "measurement error" from these data-gathering difficulties is low, and even modest-sized samples (≥10 individuals) provide reliable estimates of population parameters.

Five traits (CircNa, SnS, CloacS, TotPore, PreclPor) show high variation (CV ≥ 16%). The high variation for CircNa, SnS, and CloacS results from a high frequency of one character state and a lesser occurrence of the other states. For Pacif, CircNa is three scales for 78% of the sample, and one, two, four, and five scales for the remainder of the sample. The situation is not as extreme for SnS and CloacS, but with two scales (range 1–5) representing more than 50% of the sample for SnS, and two (~50%) and three (~30%) spurs (range 0–5) for CloacS. TotPore and PreclPor variation results from a broad range (0–26 [median 14], 0–13 [10], respectively) of pore numbers (Figure 5). The majority of adult *H. typus* have femoral pores, although this trait was not recorded during data collection; it can be calculated by subtracting PreclPor from TotPore.

Because the presence of secreting pores in adult females characterizes the unisexual *H. typus*, PreclPor and TotPore require further examination. Of the 92 Pacif adults examined, 88 individuals possessed PreclPor. The four females without pores ranged in SVL from 35.6 to 42.2 mm, well above the minimum SVL (29.2 mm) at sexual maturity. The condition of the ovaries was not recorded for the two largest individuals (40, 42 mm SVL). The 39-mm individual had small ovarian follicles, and a
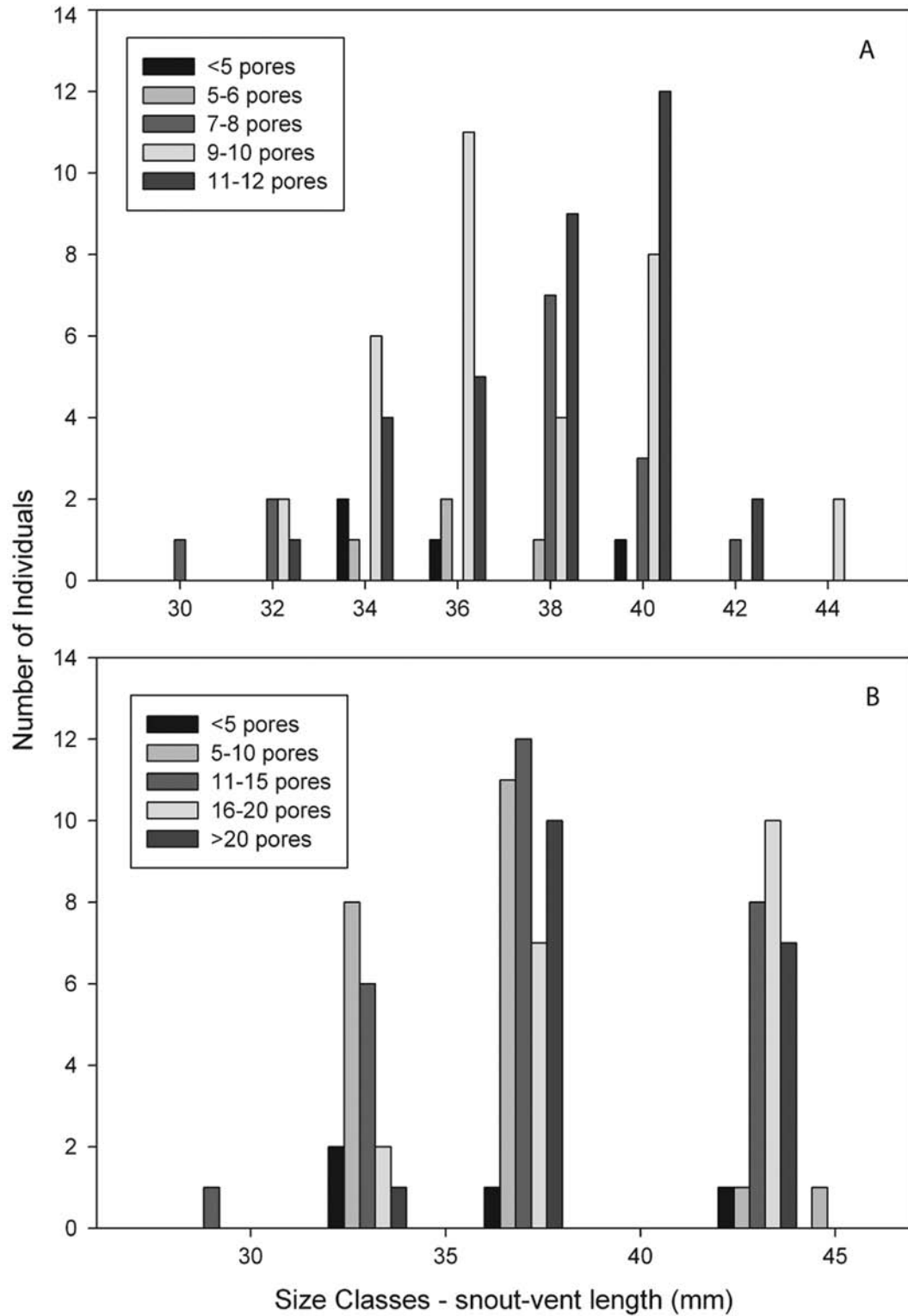
FIGURE 5. Frequency distribution of precloacal–femoral pores in the Pacific sample of unisexual *Hemiphyllodactylus typus*. Size classes are length from snout to vent (SVL) at 2-mm intervals for PreclPor and TotPore with midpoints plotted on *x* axis: (A) Precloacal pores and (B) total precloacal–femoral pores.

35-mm female had mid-vitellogenic follicles. These data indicate that all poreless individuals were mature, although the pores may have closed owing to reproductive quiescence or senescence. Both PreclPor and TotPore have broader ranges and greater variation (Figure 5) than for most other gecko species. While gathering data on *Hemiphyllodactylus*, I developed the impression that the number of pores associated with body size/maturity. Such an association is not supported by regression or correlation analyses: for example, Pearson $R = 0.074$, PreclPor to SVL; 0.27, femoral pores to SVL; 0.22, TotPore to SVL. Secreting pores occur only in adult *H. typus*; perhaps new pores develop with age and/or each successive egg development event. Precloacal and femoral pores are not continuous in any *H. typus*. Another pore trait of *H. typus* is the absence of femoral pores in some sexually mature individuals. There is no obvious pattern to their absence. Femoral pores (≥ 1) occur in the majority of adults, more or less symmetrically on left and right: Hawai 37 individuals with pores, 10 of these lack femoral pores; Polyn 6, 3; Fiji, 13, 3; NCal 9, 1; NGuin 15, 5; and Taiwan 10, 1.

Suplab, Inflab, and Chin display normal levels of variation (i.e., CV < 10%). Suplab has a median of 11 scales (range, 10–12), Inflab 11 (9–11), and Chin 11 (11–12). Dorsal (15, 13–18) and Ventral (11, 10–14) are somewhat more variable (CV = 9.8%, 10.4%, respectively). Subcaud are invariably equal-sized to adjacent caudal scales.

The *typus* digital formulae using the median value of the individual digits are 3-4-4-4 (forefoot) and 4-4-5-4 (hindfoot). Both 4FingLm and 4ToeLm are invariant, 4 and 5, respectively. Digital lamellae vary by only one scale from the median value, either 3 or 4 for 2Fing- to 5FingLm and 2ToeLm, or 4 or 5 for 3Toe- to 5ToeLm. 1FingLm and 1ToeLm have median values of 5 (4–5 1FingLm, 4–6 1ToeLm).

The Mascar sample, although considerably smaller than Pacif, shares similar medians and ranges for the scalation traits (Table 2). PreclPor differs slightly (range 4–12) and TotPore has a maximum of 17. These differences likely result from vagaries of sampling. The other difference, probably of similar origin, is the median forefoot formula of 3-4-4-3.

Sunda has a much larger *H. typus* component ($n = 40$), although as for Mascar, the pattern of variation and ranges match those of Pacif. TotPore and PreclPor share similar ranges, although the TotPore median is less, 6.5 pores. The digital formulae for the fore- and hindfoot are the same. The much smaller *H. typus* component of Philip ($n = 4$) and Sri Lanka ($n = 4$) also largely matches the medians of the Pacif sample.

Importantly, pooling adult *H. typus* from all localities ($n = 143$) yields coefficients of variation for measurements and scalation (excluding PreclPor and TotPore) that are nearly identical to CVs for the repeated measures sample. This result argues strongly for the genetic homogeneity of *H. typus* populations across the entire Indo-Pacific distribution of this unisexual taxon.

Précis. (1) The island and island group samples are homogeneous within and among samples, thereby representing a single genetic entity, *Hemiphyllodactylus typus* (Pacif). This homogeneity is shared among the unisexual components of the other regional samples – Philip, Sunda, India, and Mascar.

Unisexual—Coloration

Hemiphyllodactylus typus are not brightly colored geckos (Figure 6). Their background color ranges from a dusky tan in the light color phase to a reddish brown in the dark phase. In both phases, a series of narrow, dark brown, transverse bars or blotches lies middorsally from neck to base of tail. These bars are commonly irregularly edged, and they either extend entirely across the back or are broken middorsally. A series of moderately spaced, small light (white to creamy beige) spots lie dorsolaterally on each side of the trunk from the neck to hindlimbs. These spots are a continuation of the pre-orbital light stripe running from the naris to the anterior temporal area, ending in a brighter spot and then continuing as spots on the neck. In most instances, a dark brown stripe lies below the light stripe on the lip, fading and disappearing beyond the ear opening. The venter from chin to vent and onto tail is a dusky light tan to yellowish tan; the dusky appearance is created by a multitude of tiny dark brown spots, a few in each scale. Dorsally at the base of the tail (postsacral), a dark brown bar and abutting white to beige bar begin the irregular dark–light banding of the tail; this banding quickly becomes progressively diffuse and indistinct in most individuals.

In life, a few individuals will appear uniformly brown except for faded head markings. This situation is the common condition for preserved specimens and limited the development of quantitative coloration coding only to two characters (OrbStrp and PostocS; Appendix 1).

Neither of these two traits shows any striking variation within or among the Pacific regional samples (Table 2). Similarly there was no variation in coloration among the non-Pacific samples that was not encompassed by the description above.

Précis. *Hemiphyllodactylus typus* are predominantly dull-colored geckos. The most striking coloration
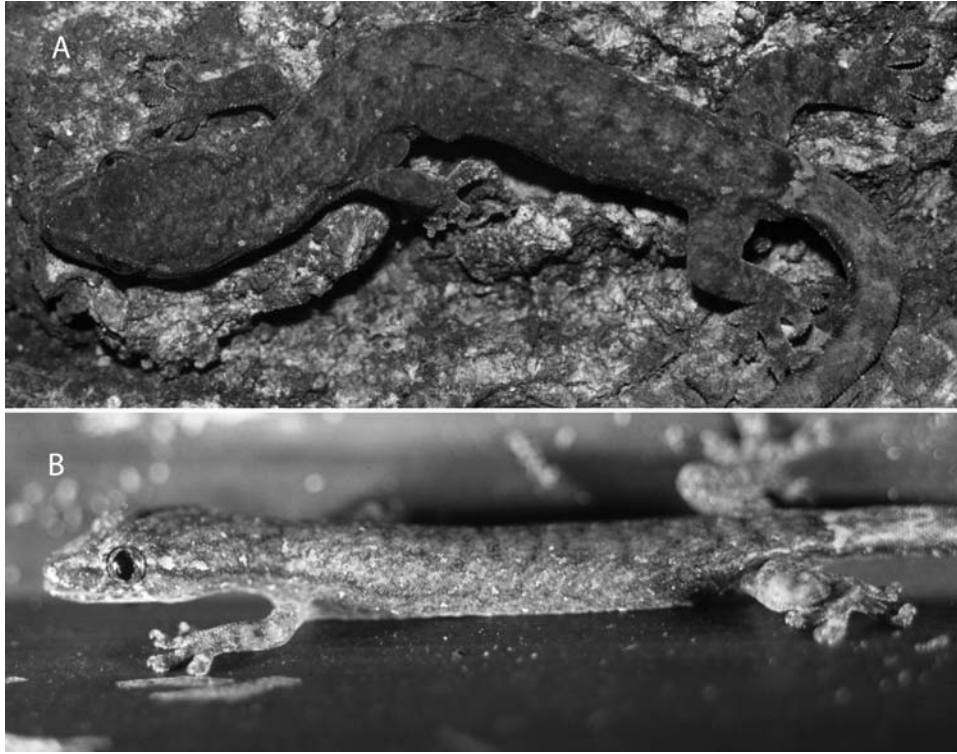
FIGURE 6. Dark and light phases of coloration in *Hemiphyllodactylus typus* from the Pacific population: (A) USNM 310814, Hawaii, Oahu (photograph by G. Zug) and (B) USNM 267979, Fiji, Viti Levu (photograph by J. R. H. Gibbons).

features are the lateral head stripe ending in a bright light spot, a series of small light spots dorsolaterally on the trunk, and bright double bar of dark and light at the base of the tail.

REGIONAL VARIATION AMONG BISEXUAL POPULATIONS

The preceding analysis of regional samples identified six samples containing bisexual individuals and populations and revealed the possibility of eight or more different bisexual populations: PALAU, PHILIP, SUNDA (potentially four bisexuals), SEAsia, CHINA, and INDIA (potentially two bisexuals).

Bisexual—Visceral Anatomy

In the bisexual samples, three (PALAU, PHILIP, INDIA) have females with pigmented caeca and oviducts (see Figure 2B). Females of SEAsia and CHINA commonly lack pigmentation on these organs; however, an adult SEAsia female (BMNH 1931.11.21.1) from Thailand has pigmented oviducts and caecum. Within the SUNDA sample, some females have the pigmented condition and others do not. I observed no differences in extent or intensity of pigmentation among the unisexual and bisexual populations. Occasionally, a female of a "pigmented" population will lack pigmentation on the caecum or oviduct. One each NGUIN and a SUNDA *H. typus* has unpigmented oviducts, and a PHILIP male and a Sri Lankan female have unpigmented caeca. In pigmented populations, commonly the peritoneum over the testes and epididymides is pigmented, although not as densely as oviducal pigmentation in females.

Most individuals identified as bisexuals in the SUNDA sample lack organ pigmentation. All SUNDA bisexuals have unpigmented caeca except three adult males from Borneo (FMNH 158734, 196268A, 213665), and the last male has pigmented epididymides. Four Sumatran females have pigmented oviducts and two of these are paratypes (IRSN 9338B, ZMA 11096) of *Hemiphyllodactylus margarethae* Brongersma.

PRÉCIS. (1) Pigmentation of caecum and oviducts is not confined to unisexual *H. typus*; this pigmentation

trait also occurs in females of the bisexual Palau, Philippines, and Indian populations, and some Sumatran females. (2) Generally, this pigmentation is absent in bisexual females of mainland Southeast Asia and the Greater Sunda Islands.

Bisexual—Morphometry

In bisexual populations, sexual dimorphism is the first morphometric issue to examine. A comparison of adult females and males in each regional sample (excluding Sunda) reveals size dimorphism in Palau, Philip, SEAsia, and China. In all four samples, females average larger than males: 32.8, 35.1, 39.0, 43.3 mm SVL, respectively; 30.6, 31.4, 35.7, 39.9 mm (Student *t* test, *P* < 0.025 for significant difference between means of females and males; see Table 3 for female ranges). Disparities in average body size result in significant differences (*P* < 0.05) for most measurements (not EyeD and SnW) in China and (not SnEye and SnW) in Palau. Philip shows dimorphism in TrunkL, HeadL, and SnEye. SEAsia shows dimorphism only for SVL. None of the proportions displays dimorphism in any sample.

Among all samples, average adult male SVL ranges from 30.3 mm (range 28.3–31.6 mm, Palau) to 39.9 mm (35.1–46.4, China). Regional variation in female morphometrics is detailed in Table 3. The two eastern mainland Asian populations (Vietnam and Hong Kong) average strikingly larger than the other mainland bisexual populations. The Palauan population has the smallest adults of any bisexual or unisexual populations. It is noteworthy that Palau, Philip, and India adult females average smaller than *Hemiphyllodactylus typus* (38.1 mm SVL; Table 3). Subsequently, I will provide some evidence for the hybrid origin of *H. typus* from the Palauan and Philippine bisexual populations.

Variation within the bisexual samples is similar to that for the regional *H. typus* samples. The CVs for measurement data (females of Palau, Philip, SEAsia, China, India) are: SVL 3.1–11.7%; TrunkL 4.3–15.2%; HeadL 3.6–12.1%; HeadW 4.1–21.4%; SnEye 5.6–13.5%; NarEye 4.3–14.9%; EyeD 5.0–13.6%; SnW 6.2–21.4%. Relative to the repeated-measure CVs, the preceding CVs are greater but only about 3% higher than observed in the repeats. Of these CV ranges, Palau females have the least variation (except SnW), Philip the lowest and SEAsia the greatest. The samples are clustered with one group (Palau, Philip, India) at the low end of the range and SEAsia and China at the high end; this clustering is consistent across all measurements. The high variation of SEAsia

and China suggests the possibility of samples containing two or more taxa. Such mixing has a probability for SEAsia owing to its geographic composition extending over 18° of latitude (Hong Kong to Chiang Mai) and 10° of longitude (length of Thailand); mixing will be examined below. India in subsequent mensural discussions consists of only Indian specimens from the vicinity of the type locality. Both Sri Lankan bisexual specimens are adults, a male (26.3 mm SVL) and a female (36.0 mm).

This disparity in size is striking. The Sri Lankan female lies within the range of other bisexual female samples (Table 3). In contrast, the male (BMNH 1910.3.16.4; 26.3 mm SVL) is nearly the smallest adult in all bisexual samples. Only one each, Indian and SEAsia males (27.2, 25.5 mm SVL, respectively), share small adult size. Even the Palau and Philip males are larger, and these two populations average the smallest in adult size of all *Hemiphyllodactylus* populations. The small size is not a mistake in the recognition of maturity, as this Sri Lankan male has 23 TotPore (16–24, range for Indian males). Although not statistically dimorphic, Indian adult females average slightly larger (35.3 mm SVL, range 33.1–37.9 mm, *n* = 6) than males (33.5 mm SVL, range 27.2–36.9 mm, *n* = 8). The proportions are nearly identical in the two sexes, thereby reinforcing the absence of sexual dimorphism within *H. aurantiacus*. The absence of morphometric differentiation between the Indian and Sri Lankan specimens was evident in the high frequency of misclassification of Indian males and females analyzed (separately) in DF analysis (a synopsis of results is in Appendix 3). The recently collected adult female and two males of *H. aurantiacus* (Bauer and Das, 1999) lie within the size ranges noted above. These authors emphasized scalation and coloration; their findings will be discussed later.

Sunda has 32 bisexual individuals (29 adults) amidst the total sample (*n* = 83). This sample visually consists of at least two bisexual taxa, and these bisexuals derive from three geographic areas (adults from peninsular Malaysia, *n* = 17; Sumatra, 8; Borneo, 3; no precise locality, 1). These samples sizes are inadequate to address mensural variation in detail; however, owing to the existence of three names (*harterti*, *larutensis*, *margarethae*), statistical examination of the mensural data is necessary. The Malaysian sample consists of nine adult females (mean 48.3, 40.9–62.1 mm SVL) and eight adult males (47.2, 35.3–56.9 mm); the smallest male (BMNH 1901.3.20.2) is the holotype of *Gehyra larutensis* Boulenger. This BMNH male is smaller than the other males (36.5–56.9 mm). The smallest female (40.9 mm) is the holotype of *Lepidodactylus Harterti* Werner (ZMB 15360). A series of 17 adults

TABLE 3. Summary statistics on select mensural characters of adult females of the bisexual *Hemiphyllodactylus* samples. The values are mean ± standard deviation (SD) and range of minimum to maximum. Organization as in Table 2, except sample sizes (*n*) are adult females, adult males, and total sample, respectively. SUNDA was excluded because it was a mixed sample of two or more taxa. Character abbreviations are defined in Appendix 1.

Character and statistic	Sample (*n*)				
	PALAU (11, 12, 24)	PHILIP (19, 17, 36)	SEASIA [a] (32, 22, 61)	CHINA (17, 18, 38)	INDIA [b] (6, 8, 17)
SVL					
Mean ± SD	32.8 ± 1.01	35.1 ± 2.87	39.0 ± 4.55	43.4 ± 3.89	35.3 ± 2.22
Range	31.1–34.2	29.6–41.3	31.9–50.5	34.9–49.3	33.1–37.9
TrunkL					
Mean ± SD	17.8 ± 0.76	18.5 ± 1.87	18.5 ± 2.82	20.9 ± 2.89	17.4 ± 1.00
Range	16.8–18.9	15.5–22.4	14.9–25.6	16.1–26.5	16.5–18.8
HeadL					
Mean ± SD	7.1 ± 0.26	7.7 ± 0.60	9.0 ± 1.09	10.1 ± 1.01	8.1 ± 0.36
Range	6.6–7.5	6.6–9.0	7.4–12.1	7.6–11.5	7.7–8.7
SnEye					
Mean ± SD	2.8 ± 0.16	3.1 ± 0.34	3.7 ± 0.50	4.3 ± 0.55	3.2 ± 0.37
Range	2.6–3.1	2.6–3.7	3.0–5.0	3.0–5.2	2.7–3.7
SnW					
Mean ± SD	1.1 ± 0.11	1.3 ± 0.08	1.5 ± 0.33	1.7 ± 0.22	1.4 ± 0.06
Range	1.0–1.3	1.2–1.4	1.0–2.3	1.3–2.2	1.3–1.4
TrunkL/SVL					
Mean ± SD	0.54 ± 0.023	0.53 ± 0.019	0.47 ± 0.033	0.48 ± 0.030	0.49 ± 0.020
Range	0.50–0.57	0.49–0.57	0.40–0.54	0.43–0.55	0.46–0.50
HeadL/SVL					
Mean ± SD	0.22 ± 0.006	0.22 ± 0.009	0.23 ± 0.013	0.23 ± 0.009	0.23 ± 0.009
Range	0.20–0.22	0.20–0.24	0.21–0.27	0.21–0.24	0.21–0.24
HeadW/SVL					
Mean ± SD	0.13 ± 0.006	0.14 ± 0.011	0.16 ± 0.018	0.17 ± 0.017	0.16 ± 0.018
Range	0.12–0.14	0.13–0.17	0.12–0.19	0.14–0.20	0.14–0.18
HeadW/HeadL					
Mean ± SD	0.59 ± 0.028	0.65 ± 0.053	0.71 ± 0.060	0.72 ± 0.063	0.71 ± 0.078
Range	0.55–0.64	0.58–0.82	0.55–0.80	0.59–0.82	0.58–0.79
SnW/HeadL					
Mean ± SD	0.15 ± 0.017	0.17 ± 0.011	0.17 ± 0.026	0.17 ± 0.012	0.17 ± 0.009
Range	0.13–0.19	0.15–0.19	0.11–0.22	0.15–0.19	0.16–0.18
OrbD/NarEye					
Mean ± SD	0.83 ± 0.049	0.83 ± 0.073	0.81 ± 0.075	0.78 ± 0.075	0.81 ± 0.067
Range	0.74–0.90	0.66–0.95	0.70–1.00	0.63–0.90	0.71–0.91

[a] The SEASIA sample includes Hong Kong specimens because of their geographic proximity to the Southeast Asian specimens and their greater geographic separation from the Yunnan specimens largely composing the CHINA sample.
[b] The INDIA sample's statistics derive exclusively from mainland Indian specimens.

from the Cameron Highlands and Fraser Hill contains the largest adult *Hemiphyllodactylus* encountered in my survey of museum collections, females ranging from 42.2 to 62.1 mm (mean ± SD, 50.2 mm ± 6.52; *n* = 8), males from 36.5 to 56.9 mm (48.1 mm ± 6.44, *n* = 7). Even though the means of the two sexes differ, there is no sexual dimorphism. This latter sample from the central mountain range (Titiwangsa) attracts attention because the named Malaysian taxa (*harterti* and *larutensis*) derive from the western mountain range (Bintang). An exploratory DFA of the two Bintang specimens and the 15 Titiwangsa ones yields 100% overall accuracy in the original classification

but only 76% accuracy in the jackknifed one (synopsis of results in Appendix 3). Classification function assignments indicate differences in head shape by identifying HeadL, HeadW, NarEye, Eye D, and SnW as the major variables in the classification function. A DFA of mensural proportions yielded lower classification accuracy, indicating no differentiation value.

The Sumatran specimens are one adult male (38.8 mm) and seven adult females (41.2, 36.0–46.9 mm). This sample includes the four type specimens of *Hemiphyllodactylus margarethae* Brongersma: two adult females (42.0 mm, ISRN 9338B; 46.9 mm, ZMA 11096), a juvenile male (38.0 mm, IRSN 9338A), and an adult male (38.8 mm, holotype ZMA 11095). The Bornean sample consists of three adult males (33.2 mm, 27.8–37.3). The final Sunda bisexual is an adult male (38.6 mm) of uncertain provenance in the East Indies.

Sunda adults do not display sexual dimorphism in any mensural or proportional trait. The preceding description of size differences in the three regional subsamples suggests the possibility of size dimorphism in the Malaysian sample (i.e., females larger but not statistically significantly so) and regional differences (smaller adults in Borneo, although the *H. larutensis* holotype is small also).

The SEAsia sample shows dimorphism in only SVL of the mensural and proportional traits. In compiling this sample, I assumed that specimens from Thailand eastward through Vietnam and South China represented a single population or taxon, hence potentially recognizable as *H. chapaensis* (Bourret). The initial analysis of morphometrics and the general similarity (means differ but strong overlap of ranges occurs) of the China and SEAsia samples (Table 3). indicated that my assumption was incorrect and required testing. Another question on the uniformity of the SEAsia sample arises from the broad longitudinal breadth (99°–115° E) of the sample, extending from Chiang Mai in the west to Hong Kong in the east. The latitudinal depth of the sample is much less, approximately 7° (19°–12° N). The China sample (assumed to represent *H. yunnanensis*) is broad but nonetheless not as geographically expansive as SEAsia and limited to the "highlands" (Shan and Yunnan plateaus).

To test the preceding assumption of homogeneity between and within these two samples, I examined them in several ways: (1) variation within a combined China-SEAsia sample and (2) the subdivision of these two samples into various subsamples and comparison of the subsamples. The combined China-SEAsia sample contains 48 adult females and 39 adult males. Student *t* tests of all mensural and proportional traits show that

size dimorphism persists in most dimorphic traits (SVL, TrunkL, HeadL, HeadW, SnEye, NarEye) identified in the China sample and additionally the proportions EyeD/HeadL and EyeD/NarEye. Typically, the *p* values for the *t* test are slightly higher in the combined sample (e.g., SVL *P* = 0.008, 0.019, China versus combined). Even though the SEAsia sample is the larger of the two, its absence of dimorphism did not swamp the average size difference of females larger than males.

The combination of these two samples, however, results in a near doubling or more of CV of most mensural traits as compared with the China sample. This increased variation reflects a mixing of two or more phenotypes, presumed here to represent distinct genetic entities. A combination based on topography (China [contains only Yunnan and Shan plateau specimens] and the highland areas of northwestern Thailand [Tak to Mae Hong Song and Chiang Rai]) did not alter combined sample variation (i.e., CVs equivalent to those of China alone). The mean SVL of this China-Thai sample decreased from 43.3 mm (China) to 40.7 mm, but the mean values of all proportions of the two samples are less than 1% different, supporting the homogeneity of *Hemiphyllodactylus* from this region. Addition of the northern Vietnam (Chapa area) specimens to the China-Thai sample did not alter means or CVs; similarly, the addition of Hong Kong specimens did not alter the level of variation. These additions of a few individuals to a large (*n* > 30) sample are, however, unlikely to alter CV unless a striking disparity exists in the added sample.

The realignment of China and SEAsia specimens suggests the existence of a northern (upland) population and a southern one ("lowland" Thailand only in the present sample). The latter averages smaller than the former (Table 4). The situation (affinities) of other Southeast Asian specimens is unclear owing to small samples (Table 4). The Vietnam *chapaensis* sample averages larger (SVL) than the four other samples, but its range is within that of the China–NW Thailand sample. Its proportions similarly match the latter sample's proportions. The Laos sample is the smallest (*n* = 2) of this comparison, hence difficult to interpret, and a single male from Cambodia is immature. Presently, I note only the low TrunkL/SVL proportion representing a shorter trunk length than in the other Oriental samples. Interestingly, they appear less robust than the Hong Kong *Hemiphyllodactylus*, whose general appearance matches the stouter habitus (Figure 3) of large adult female *H. yunnanensis*; yet they have a longer trunk (53% TrunkL/SVL, Table 4) similar to the taxa with the slender habitus. A DFA of Oriental adults using

TABLE 4. Summary statistics on select metric characteristics of adults of the bisexual *Hemiphyllodactylus* from southern Asia. The values are mean ± standard deviation (SD) and range of minimum to maximum. Realigned and restricted regional samples from the CHINA and SEASIA samples: CHINA–northwestern Thailand; Thailand, area exclusive of the northwest; Laos, Phong Saly; Vietnam, *chapaensis* type locality; and Hong Kong. Sample sizes (*n*) are total adults, females, and males, respectively. Character abbreviations are defined in Appendix 1.

Character and statistic	Sample (*n*)				
	CHINA–NW Thailand (61, 33, 28)	Thailand (16, 9, 7)	Laos (2, 1, 1)	Vietnam (3, 3, 0)	Hong Kong (4, 2, 2)
SVL					
Mean ± SD	39.4 ± 4.68	35.1 ± 2.77	37.1 ± 0.78	46.2 ± 3.16	43.0 ± 6.13
Range	25.5–49.3	30.0–39.9	36.5–37.6	42.7–48.8	35.3–50.3
TrunkL/SVL					
Mean ± SD	0.47 ± 0.031	0.47 ± 0.036	0.42 ± 003	0.49 ± 0.011	0.53 ± 0.032
Range	0.40–0.55	0.42–0.52	0.42–0.43	0.48–0.51	0.51–0.58
HeadL/SVL					
Mean ± SD	0.23 ± 0.010	0.23 ± 0.014	0.24 ± 0.005	0.23 ± 0.004	0.22 ± 0.007
Range	0.21–0.26	0.21–0.26	0.23–0.24	0.23–0.24	0.21–0.23
HeadW/SVL					
Mean ± SD	0.17 ± 0.018	0.17 ± 0.017	0.17 ± 0.002	0.17 ± 0.002	0.16 ± 0.010
Range	0.14–0.22	0.14–0.20	0.16–0.17	0.17	0.15–0.17
SnEye/HeadL					
Mean ± SD	0.41 ± 0.025	0.41 ± 0.026	0.39 ± 0.024	0.42 ± 0.023	0.41 ± 0.0.37
Range	0.34–0.46	0.38–0.46	0.37–0.42	0.40–0.44	0.38–0.46
SnW/HeadL					
Mean ± SD	0.17 ± 0.020	0.16 ± 0.025	0.21 ± 0.008	0.17 ± 0.002	0.16 ± 0.015
Range	0.11–0.22	0.12–0.20	0.20–0.22	0.16–0.17	0.15–0.18
SnW/HeadW					
Mean ± SD	0.24 ± 0.036	0.22 ± 0.035	0.30 ± 0.001	0.24 ± 0.007	0.22 ± 0.014
Range	0.15–0.36	0.16–0.29	0.30	0.23–0.24	0.21–0.24

all 10 proportions yields a poor classification (jackknifed) of these subsamples; all were classified at ≤50% (synopsis of results in Appendix 3). Larger samples are essential to address these confusing morphometrics.

Zhou et al. (1981) described three subspecies of *H. yunnanensis* from China without reference to any other species or populations of *Hemiphyllodactylus*. They had good samples (≥20 individuals) for each subspecies, and although they reported some measurements (Table 5), they presented no statistical analysis and no mensural data for the nominate subspecies. The westernmost subspecies (*H. y. longlingensis*) is the smallest of three forms and shares the range of my Yunnan sample. The two eastern forms (*H. y. dushanensis* and *H. y. jinpingensis*) are distinctly larger geckos than the western ones. Their adult SVLs (Table 5) do not overlap with either *H. y. longlingensis* or the Yunnan sample. TrunkL/SVLs of the east and west

forms also do not overlap, but surprisingly HeadL and SnEye do. This overlap suggests that either these forms/populations have proportionally smaller heads or there was a lack of precision in recording these measurements. All three of these subspecies show strong sexual dimorphism in SVL with only *H. y. longlingensis* showing a slight overlap of the largest male and smallest female. The absence of overlap suggests that the specimens examined (and reported in the tables) underwent selection prior to analysis because of the strong overlapping ranges of adult females and males in my CHINA sample, even though the average SVLs are significantly different.

As an aside, one Thailand adult or near-adult *Hemiphyllodactylus* (BPBM 3502, Sakaerat) is hermaphroditic, with large testes and a pair of vitellogenic follicles (maximum diameter 3.2 mm). All other unisexual and bisexual specimens examined had gonads of only one sex.

TABLE 5. Comparison of some character measurements of adult females among the Chinese populations of *Hemiphyllodactylus yunnanensis*. Data for the subspecific samples of *H. yunnanensis* were derived from Zhou et al. (1981: tbls. 2–4). Character abbreviations are defined in Appendix 1; a dash (-) means no data were available.

	Length (mm) range for sample or subspecies (*n*)				
Character	Yunnan (12)	*yunnanensis*[a] (0)	*longlingensis* (19)	*jinpingensis* (10)	*dushanensis* (10)
SVL	37.2–48.8	-	39.0–46.0	49.0–53.5	48.0–51.0
TrunkL	17.4–23.4	-	20.0–23.5	24.0–28.5	25.0–27.0
HeadL	8.8–11.4	-	9.0–10.0	10.5–11.0	10.0–11.0
SnEye	3.7–5.1	-	4.0–5.0	4.5–5.0	5.0–5.5
ForelimbL	-	-	10.0–12.0	11.0–12.0	11.0–12.0
HindlimbL	-	-	13.0–16.5	16.0–17.5	16.0–17.5

[a] Despite a sample of 249 specimens, no measurements were reported by Zhou et al. (1981) in the description of *H. y. yunnanensis* nor was a table of measurements provided. Measurements also were not included in the descriptions of the new subspecies.

PRÉCIS. (1) Morphometry is only modestly useful in the differentiation of intra- and interregional samples of the bisexual populations. (2) PALAU, PHILIP, and CHINA display size dimorphism between adult females and males. Females average significantly larger than males. (3) The Palauan population has the smallest average SVL of all populations. The Philippine and Indian-Sri Lankan populations are also small but average significantly larger than the Palauan one. Average size of the CHINA and SEAsIA samples is significantly larger than the preceding three samples. (4) The original composition of INDIA, SEAsIA, and SUNDA each probably includes representatives of at least two taxa/populations. INDIA contains an Indian component (*H. aurantiacus*) and a Sri Lankan one (unnamed). Inclusion of northwestern Thailand specimens in the CHINA population does not increase variation, thus suggesting genetic homogeneity among these "highland" populations. The remainder of the SEAsIA sample potentially remains a mixed sample. Presently, there are insufficient museum specimens for a fine-scale geographic analysis. This problem is also shared by SUNDA, which clearly has multiple taxa therein.

Bisexual—Scalation

Sexual dimorphism in PreclPor and TotPore is shared by all samples. Adult males have secretory pores; females do not or do so uncommonly. Females with secreting pores occur in all Asian samples. The sample INDIA-India contains a single adult female (BMNH 74.4.1332, a syntype of *H. aurantiacus*) with three PreclPor, about half the number found in males (Table 6). CHINA has three females with pores, one with only seven precloacal pores, another with nine precloacal pores separated from one femoral pore on each side, and a final individual with a continuous precloacal–femoral series of 19 pores. SEAsIA also has three pore-bearing females; the holotype of *H. t. chapaensis* has nine PreclPor, and two Thai females have continuous series of 14 and 15 pores. In SUNDA, pores occur only in Sumatran females, two of seven individuals (12 PreclPor in one and separate series of 9 and 20 in the other). Generally, but not always, TotPore is distinctly less in females than in males. No other scalation traits show dimorphism in PALAU, PHILIP, SEAsIA, CHINA, or INDIA. The composite nature of SUNDA does not permit rigorous testing for dimorphic traits.

Most scalation traits are fairly uniform across the six bisexual samples (see Table 6, although SUNDA not included). I present medians because the data for scalation traits are discontinuous values and integers better portray the actual number of scales than does a decimal value. The uniformity among samples is most evident in the overlapping ranges of minimum and maximum values. Among the six samples, CircNa is identical (three scales) in all samples. SnS ranges strongly overlap amidst the six samples with SEAsIA individuals typically possessing only two "internasal" scales, and PALAU and INDIA each with four SnS. This latter condition and the three-SnS one represents a large "supranasal" above the naris on each side separated medially by two or one small scales. Inflab are similar with most samples having ten scales, PALAU with nine and INDIA-India with 11. Most samples have 10 Suplab, with 8 for PALAU and 11 for SUNDA. Although these differences (for Suplab, but other traits as well) are slight

TABLE 6. Summary statistics on select coloration and scalation characters of juveniles and adults of the bisexual *Hemiphyllodactylus* samples. Organization as in Tables 2–4. Sample sizes (*n*) are juveniles, adults, and total sample, respectively. Statistical values are either median ± standard deviation (SD) and range of minimum to maximum (for coloration and scalation characters) or modes and frequency (%) of occurrence (for finger and toe lamellae). Character abbreviations are defined in Appendix 1.

Character and statistic	Sample (*n*)				
	PALAU (11, 12, 24)	PHILIP (15, 19, 35)	SEAsia [a] (32, 22, 61)	CHINA (17, 18, 38)	INDIA [b] (6, 8, 17)
PostocS					
Median ± SD	4 ± 0.88	3.5 ± 1.18	1 ± 1.38	2 ± 1.41	0 ± 2.17
Range	2–6	0–6	0–4	0–5	0–7
SnS					
Median ± SD	4 ± 0.65	3 ± 0.48	2 ± 0.68	3 ± 0.72	4 ± 0.89
Range	3–5	2–4	1–4	2–5	3–6
Suplab					
Median ± SD	8 ± 0.78	10 ± 1.15	10 ± 0.91	10 ± 0.70	10 ± 0.89
Range	8–11	8–13	8–12	9–12	10–13
Chin					
Median ± SD	11 ± 0.90	11 ± 1.52	8 ± 1.59	8 ± 1.38	11 ± 1.12
Range	9–12	8–14	6–18	6–11	10–14
Dorsal					
Median ± SD	15 ± 1.44	15 ± 1.50	14 ± 1.78	13.5 ± 1.80	13 ± 1.87
Range	11–18	12–18	9–18	12–17	11–17
CloacS					
Median ± SD	2 ± 1.01	2 ± 1.89	1 ± 0.69	1 ± 0.38	2 ± 0.63
Range	1–4	0–3	0–4	1–2	1–3
TotPore [c]					
Median ± SD	22.5 ± 8.15	27 ± 5.35	21.5 ± 4.28	19 ± 3.31	21.5 ± 2.91
Range	16–28	17–38	11–26	11–24	16–25
4ToeLm					
Median ± SD	4 ± 0.38	4 ± 0.41	3 ± 0.80	4 ± 0.42	3 ± 0.46
Range	4–5	4–5	3–5	3–5	2–3
FingerLm [d]					
Modal values	3-4-4-3	3-3-3-3	3-3-3-3	3-3-3-3	2-2-2-2
Frequency	55.0%	65.7%	72.2%	36.8%	100%
ToeLm [d]					
Modal values	3-4-4-4	3-4-4-4	3-3-3-3	3-4-4-4	2-2-3-2
Frequency	45.8%	50.0%	50.1%	57.9%	37.5%

[a] The original composition of CHINA and SEAsia samples is retained for consistency of comparison with Table 4 and mensural results described and discussed earlier in the text and tables.
[b] The values are only for the mainland India portion of the INDIA sample.
[c] These values are only for the adult male portion of each sample.
[d] Lamellae formulae represent the most frequent formula (mode) for each sample and the percent of the sample with this formula (frequency).

and usually not statistically significant, I suggest the differences reflect genetic differentiation among the regional populations and are not the result of sampling or measurement error. This proposition derives from the relatively low variation (CV) observed for most scalation traits (see the earlier Baseline Estimates section). The re-aligned

CHINA–NW Thai sample usually has the same medians as CHINA and similar standard deviations

Chin ranges strongly overlap; however, the low medians (8) of SUNDA, SEAsia, and CHINA result from six or seven scales in most individuals and the higher medians of PALAU, PHILIP, and INDIA from most individuals having
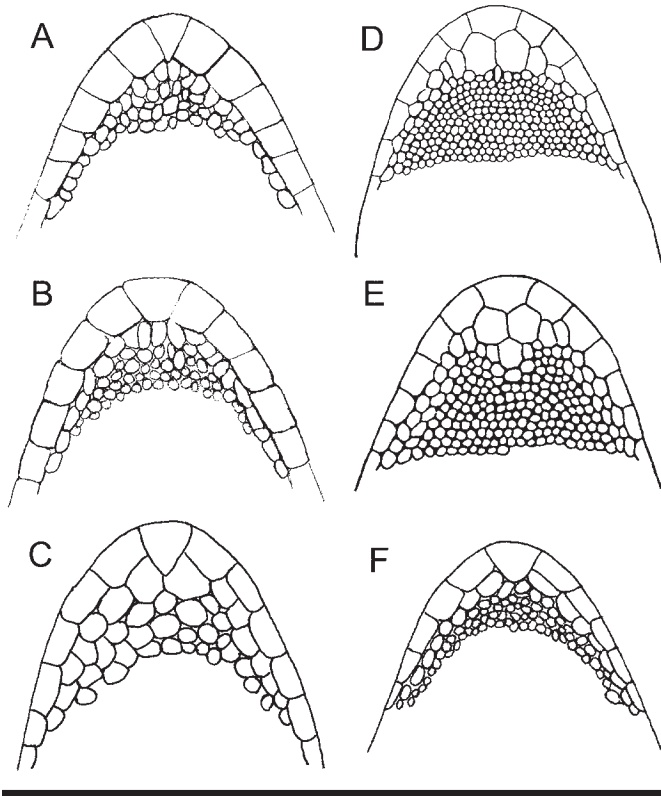
FIGURE 7. Scale morphology of the chin in various populations of *Hemiphyllodactylus*: (A) *H. typus* USNM 570742 Hawaii; (B) *H. ganoklonis* USNM 563682 holotype, Palau; (C) *H. margarethae* ZMA 11095 holotype, Sumatra (redrawn from Brongersma 1931: fig. 4); (D) *H. y. yunnanensis* China (from Zhou et al., 1981: fig.4 left); (E) *H. y. longlingensis* China (from Zhou et al., 1981: fig.4 right); (F) *H. chapaensis* NMHN 1948.43 holotype, Vietnam (redrawn from Bourret, 1937: fig. 1b).

10 or more chin scales. The difference in total number of scales in the chin scale arc results from the enlargement of the two median scales posteriorly bordering the mental (i.e., postmentals). Postmental shape and size are variable within each Asian sample; nonetheless differences in postmental size serve to delimit southern Asian populations and denote populational differentiation.

Beginning in the north with populations identified as *H. yunnanensis* (CHINA), each postmental is one-third to half the area of the first supralabial (Figure 7D,E); the laterally abutting chin scale is commonly one-third to two-thirds the area of the postmental and distinctly larger than chin scales behind and beside it. This anteriormost row, including the postmental, is an arc of larger scales, and posteriorly the chin scales quickly decrease in size to granular scales. In CHINA, the mental is modestly large and

roughly an equilateral triangle to a flattened pentagonal shape. In SEAsia, the chin scale condition is as described above, although I have the impression that the next posterior scale row to the "large" scale arc has proportionately larger scales than my CHINA specimens and then a rapid diminution to granular chin scales. I note no substantial difference from the preceding pattern for individuals from Hong Kong to northwestern Thailand.

Interestingly, my examination of the holotype of *H. chapaensis* revealed a low Chin (seven scales), hence a modestly enlarged postmental, but Bourret's (1937:60) description noted the postmentals as "une paire de très petites plaques." His illustration (reproduced in Figure 7F) shows an arc of enlarged chin scales with postmentals not much larger than the posterior chin scales. This morphology contrasts to Hong Kong *H. chapaensis* (so taxonomically labeled by Lazell, 2002), which possess large postmentals followed by a second arc of enlarged (although not as greatly) chin scales. A southern Vietnamese specimen (USNM 146161) has very large, rectangular postmentals similar to those depicted for *H. margarethae* (Figure 7C). The Cambodian male (FMNH 270569) has an arc of nearly equal-sized scales (Chin = 10). All SUNDA specimens have large, rectangular postmentals. For most and the above-mentioned Vietnamese specimen, the postmentals broadly contact medially, and posteriorly chin scales rapidly decrease in size (Figure 7).

Dorsal and Ventral, each, have overlapping ranges among the six samples. The pattern of variation between these two traits is different. Note that the number of scales for each derives from the EyeD distance; thus the values represent the number of scales within the same area for each specimen, although there may be an increase in variance within a sample owing to the manual measurement of EyeD. The CV is 12–15% and in the same range as Chin and most finger and toe lamellae counts. Dorsal values have identical (or nearly so) medians (14% and 15%) for all samples except INDIA-India, which is distinctly lower (12%; Table 6). For Ventral, the medians are more variable. SUNDA, SEAsia, and CHINA have eight scales, PALAU and INDIA 10, and PHILIP 11. The Sundan to Chinese populations have proportionally larger ventral scales compared both to dorsal scales within individuals and to the ventral scales of Pacific and Indian specimens.

CloacS ranges from absent to four spurs in the total bisexual sample (Figure 8). Part of this variation is due to sexual dimorphism, with females tending to have fewer or no spurs (statistically significant only in PALAU and PHILIP); nonetheless, there are populational differences, with SEAsia and CHINA individuals averaging a single
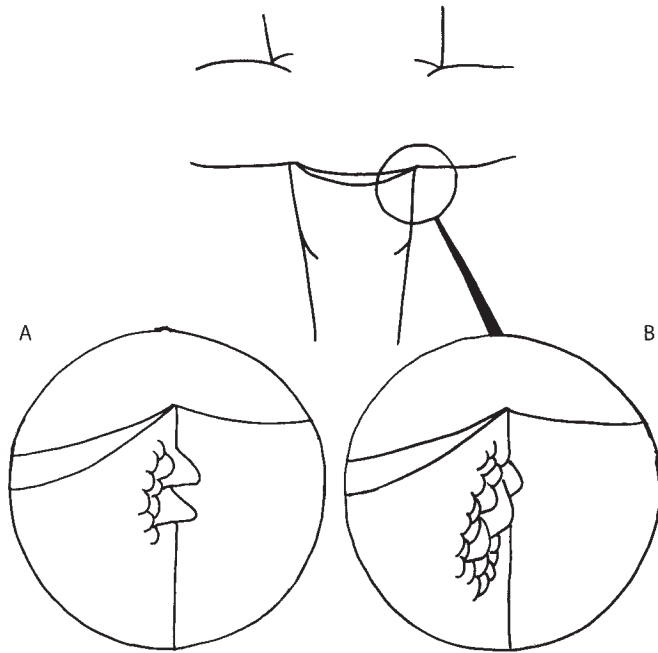
FIGURE 8. Cloacal spur morphology in *Hemiphyllodactylus*: (A) Pinted state, *H. yunnanensis*, Thailand (USNM 310807); (B) rounded stated, *H. typus*, Hawaii (USNM 279240). Illustration by J. Kilby.

FIGURE 9. Digital lamellae morphology in select species of *Hemiphyllodactylus*: (A) Right hindfoot, *H. yunnanensis*, Thailand (USNM 310807); (B) right forefoot, *H. yunnanensis* China (BMNH 1904.11.29.10D); (C) right hindfoot, *H. typus* Hawaii (USNM 27924); (D) right hindfoot, *H. yunnanensis* China (BMNH 1904.11.29.10D). Illustrations by J. Kilby.

spur. This average or median value is not driven by a larger number of females in the samples, as the number of adult females nearly equals the number of males in all samples.

In most populations the median row of ventral scales on the tail (Subcaud) equal the size of adjacent scales. Only in a few individuals and only in the SUNDA, SEAsia, and INDIA samples are Subcaud slightly enlarged over adjacent scales. No *Hemiphyllodactylus* has enlarged subcaudal scales like those of many *Gehyra* species.

Finger and toe lamellae counts (Table 6; Figure 9) are relatively uniform among all samples except for INDIA. Individuals of the latter population have distinctly fewer enlarged U-shaped subdigital lamellae on the fore- and hindfeet. This difference is strikingly apparent; the fore- and hindfoot lamellae formulae (second through fifth digit of each foot) of INDIA is 2-2-2-2, 2-2-3-2, contrasting to the modal 3-4-4-3, 3-4-4-4 of the other Asian samples. The modality of these formulae, however, is 3-4-4-4 and 4-5-5-4 in the Vietnamese, Hong Kong, and Cambodian specimens and 3-4-4-4 and 4-5-5-5 for the SUNDA Titi-wangsa specimens.

As with the mensural characters, it is necessary to comment on the Zhou et al. (1981) study of Chinese

Hemiphyllodactylus populations. Their scalation data examined seven traits: rostral notched posteromedially, enlarged scale posteriorly bordering "supranasal," Suplab, Inflab, chin scale bordering mental posteriorly (postmentals)], digital lamellae formulae, and precloacal–femoral pores. The pore condition is examined later. I did not score/record either of the first two traits. My initial research in unisexual *Hemiphyllodactylus* populations indicated that a rostral notch was always present although of variable development (i.e., indistinctly notched to cleft one-third length [rarely] of rostral scale); hence this trait was not included in my character set. The variation in the relative size of the post "supranasal" scale completely escaped my attention. Zhou et al. used the relative size of the postmental scales, in part, to differentiate *H. y. yunnanensis* and *H. y. longlingensis*. I have not seen specimens from the range of *H. y. longlingensis*; however, four *Hemiphyllodactylus* (USNM 570732–570735) from the western edge of the Shan Plateau (Myanmar) match the enlarged second arc of chin scales shown for *H. y. longlingensis* (Figure 7) with the exception that in the four Burmese specimens, the chin scales are more uniform in size and the median one is no

larger than its laterally abutting scales in the arc. Because my CHINA sample derives largely from Kunming, my results match the Zhou et al. concept of *H. y .yunnanensis*. My results for Suplab and Inflab similarly match their data.

Their data for digital lamellae, however, contrast sharply to mine. Foremost is low variation in their counts compared with mine. Deciding which lamellae is the proximalmost one on each pad can be challenging owing to a gradual reduction in size proximally. My protocol to increase the consistency (precision) of my counts is/was to count only the distinctly U-shaped lamellae. Comparison of my China formulae to their *H. y. yunnanensis* formulae yields five forefoot formulae (2-3-3-3, 3-3-3-3, 3-4-4-3, 3-4-3-3, and 3-3-4-3; the second and third formulae represent 37 and 21%, respectively, of the sample) versus two formulae in Zhou et al. (3-4-4-3, 3-4-4-4; they do not present the frequency of occurrence of each), I recorded nine different hindfoot formulae (ranging from 3-3-3-3 to 4-5-5-5) with 3-4-4-4 in 60% of the sample, occurrence of others is ≤10%, usually much less, versus an invariant 3-4-4-4 reported by Zhou et al. I, obviously, believe that my data more accurately reflect the natural variation of the Yunnan population. My data cause me to question the discriminatory potential that Zhou et al. attributed to these formulae for the differentiation of populations within their broader China sample. Digital formulae do discriminate populations (e.g., compare INDIA to the other five bisexual samples [Table 6]), but the validity of the Zhou et al. data requires an independent study.

Precloacal–femoral pore morphology is similar in medians (19–22.5) and range of (11–28) of TotPore (Table 6) for PALAU, SEAsia, CHINA, and INDIA. PHILIP has a distinctly higher median TotPore and a partially overlapping range, although extending well beyond the upper limits of the four former samples. The medians and ranges of PreclPor for the preceding five samples are more similar to one another (median range 7.5–11), presumably owing to all geckos having proportionally the same pubic or escutcheon area for pore development. Higher or lower TotPore counts derive mainly from an increase or decrease in the length of the femoral pore series.

Number of pores, however, disguises two pore morphologies (Figure 10): (1) continuous series of precloacal and femoral pores and (2) separate longitudinal patch of precloacal and femoral pores. The continuous pore morphology occurs in all males of SEAsia and CHINA samples and the separate-patch morphology in all males of PALAU, PHILIP, and INDIA (including a single Sri Lankan male) samples. The relative size of the pore scales appears identical in the two morphologies. In some SEAsia males (e.g., USNM 146161, southern Vietnam), the pore scales are separated by one (usually) or two smaller (one-third or less pore scale area) scales. From the low frequency of this condition and the very few specimens from southern Vietnam through southern Thailand, it is uncertain whether this condition is a variant or populational state.

Pore morphology in SUNDA shows regional differentiation with the occurrence of both continuous-patch and
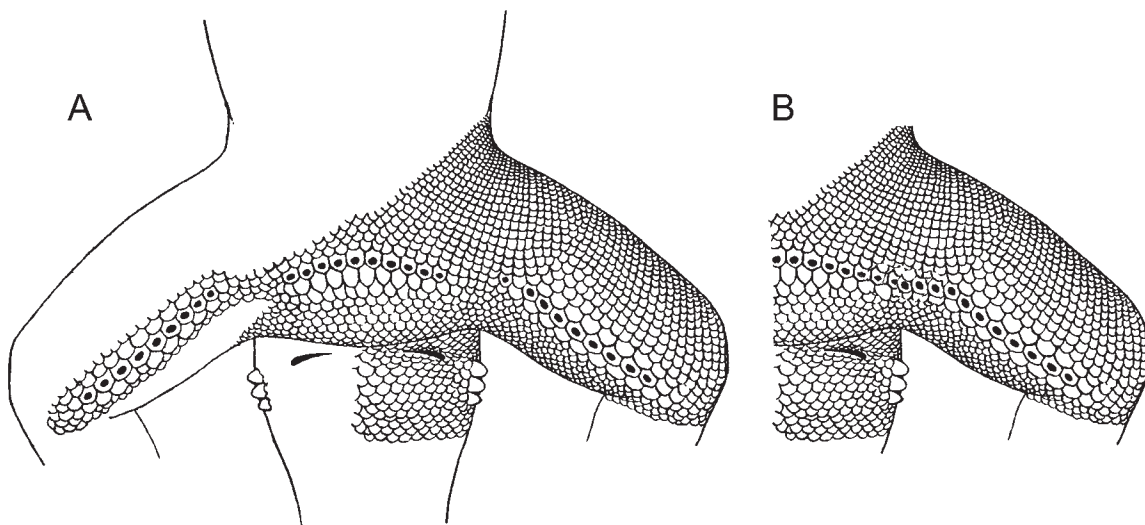

FIGURE 10. Schemata of precloacal–femoral pore morphology of *Hemiphyllodactylus*: (A) Separate pore series and (B) continuous pore series. (A modified from and B reproduced from Taylor, 1918: fig. 4; *H. insularis*.)

separate-patch states, each state apparently occurring at a specific location. Even though sample sizes of the various islands or sites are small, the differences among localities are suggestive of genetic differentiation of populations. Sumatran and Bornean adult males (*n* = 1, 3, respectively; median TotPore 26, 29) have the separate-patch state; further as noted in discussion of sexual dimorphism, some adult females from these two islands possess precloacal pores and occasionally femoral pores. Malaysian males have continuous precloacal–femoral series with a lower median TotPore (21, 17–39; Titiwangsa specimens only, *n* = 7). The presence of these two states in SEAsia is nomenclaturally important because of three available names. The *H. margarethae* holotype has the separate-patch state, the male *G. larutensis* holotype a continuous state, and the female *L. Harterti* holotype lacks pores.

PRÉCIS. (1) Sexual dimorphism of scalation occurs only in the presences (males) and absences (females) of precloacal and femoral pores. (2) Most scalation traits are uniform throughout the Asian and Pacific Rim populations. Difference among samples is evident in the characters of Chin, Dorsal, Ventral, digital lamellae, and precloacal–femoral pore. (3) Chin shows two states: enlarged chin scales (postmentals) in SUNDA, SEAsia, and CHINA and no postmentals in PALAU, PHILIP, and INDIA. (4) INDIA has large dorsal trunk scales, only slightly smaller than the ventral ones; all other samples display a greater size difference between dorsal and ventral scales and typically more scales per unit area. (5) Digital lamellae formula is strikingly lower in INDIA than in the other five regional samples, and the formulae in the latter samples are the same. (6) Pore morphology differs with CHINA, SEAsia, and some SUNDA populations with continuous series of precloacal–femoral pores and PALAU, PHILIP, some SUNDA, and INDIA with separate patches of pores.

Bisexual—Coloration

The drab, presumably cryptic, coloration of *Hemiphyllodactylus* makes characterization of coloration difficult. I recorded two external coloration characters: PostocS and OrbStrp. The results show regional differences. For example, PALAU and PHILIP have higher median PostocS (Table 6) in contrast to the median of one or two postocular spots for SEAsia, CHINA, and INDIA; however, the ranges for these five localities are the same. The "identical" ranges reflect the difficulties of seeing these spots in older or poorly preserved specimens. If an actual difference exists, it will require documentation with living specimens or recently preserved ones. OrbStrp is less likely

to disappear with the age of a specimen owing to its dark pigmentation; nonetheless, old specimens fade to unicolor and this trait can be lost also. My data (Table 5) suggest the near universal presence of OrbStrp in bisexual specimens, at least to the level of the ear.

With my attempt at quantification of coloration ill-founded for museum specimens, I offer a comparative descriptive approach using the major pattern features identified in the *H. typus* coloration section. These descriptive data derive from my notes on museum specimens, descriptions and illustrations from herpetological literature, and field notes of mine and others sources are noted in brackets.

Coloration is variable locally within populations and broadly throughout the distribution of bisexual populations. Dorsal ground color for all populations is variously described as tan to grayish brown. The intensity of the "brown" background depends on the color phase, light or dark, assumed at death and preservation or when photographed. The phase also affects the conspicuousness of markings, whether they are light (usually off-shade whites to tans) or dark (brown to nearly black-brown). The venter also lightens and darkens, hence ranges from near-white to dusky; because each scale normally shows tiny spots (melanophores), the venter is never white. The following descriptions will emphasize five areas: (1) loreal or snout area, (2) side of head and neck (ignoring the lightening resulting from accumulation of calcium carbonate in the endolymphatic system), (3) dorsal and lateral trunk, (4) sacrum and base of tail, and (5) sides and top of tail.

Several traits are shared by most individuals of the bisexual populations. Intensity and color vary from population to population. A dark brown lateral stripe extending from the loreal area to at least the anterior quarter of the neck occurs widely, although its thickness and loreal development are variable. For example, in a series of northwestern Thai specimens, the loreal stripe ranges from a dark spot immediately in front of the eye through a well-defined stripe from naris to eye to a fully dark brown loreal area. Similarly behind the eye, the lateral stripe (OrbStrp) ranges from narrow to broad (always above the ear opening), terminating at head–neck juncture or anywhere from this juncture to the shoulder. A dark lateral stripe is variously evident on the trunk, and if present, it is typically moderately broad but irregularly edged above and below, occasionally bordered above by a broad lighter area. Often this stripe breaks into a series of dark blotches.

Dorsally, the head is unicolor or nearly so with a faded and diffuse mottling. The back is similar, ranging from unicolor through small, paired parasagittal dark spots to

broad, irregular dark brown bars (continuous across the midline or interrupted). Most individuals display a signature mark posteriorly from the sacrum onto base of the tail. This mark contains a (supracloacal) middorsal dark blotch bordered posteriorly by a (supravent) light mark that can have anterior extension on each side of the middorsal dark blotch with the anterior arm usually ending at the top of the ilium, hence a U-shaped light mark. This contrasting dark and light postsacral mark is often the brightest area of coloring of a *Hemiphyllodactylus*. Posteriorly the top and sides of the tail range from light to medium brown, nearly unicolor to distinctly banded. In life, the underside of the tail is variously reported as shades of red or orange.

Palau *Hemiphyllodactylus* are generally drab lizards with the exception of the bright postsacral signature mark. Ground color is light gray to tan. The dorsal pattern ranges from a sparse speckling of dark brown spots to small, irregular V- or trident-shaped bars. A dorsolateral row of widely spaced pinkish yellow spots extends from the rear of the head to the postsacral mark; the spots on the posterior third of the trunk are the most prominent ones. The postsacral mark has a small dark middorsal spot (roughly triangular) encompassed by a broad-based U-shaped light pink mark, which is bordered laterally on each side by a diffuse dark dorsolateral stripe (Figure 11). The tail ranges from yellow to tan with diffuse midline dark marks and narrow light pink transverse bands. In the loreal region, a preorbital stripe is always present but generally only moderately developed, ranging from a dark preorbital spot to a narrow stripe extending midway to the naris. The postorbital stripe is narrow, always fragmented, and often only with a few fragments on the side of head, somewhat more extensive on the neck to the shoulder. (Coloration is reported from Ronald I. Crombie's [RIC] unpublished 1993–2002 field data notes and my personal observation of color in RIC's images and preserved specimens.)

Philip *Hemiphyllodactylus* are similar to Palau ones with light to medium brown backgrounds. The dorsal pattern ranges from a faint dark flecking or reticulation through paired, parasagittal dark longitudinal dashes to small dark blotches. Dorsolaterally, a row of brick red, dark-edged spots occurs on each side from behind eye to and onto tail. The postsacral mark has a brown V-shaped anterior border to the broader red U-shaped portion; the latter is usually strongly edged in brown laterally and posteriorly. Tail is lightly colored, presumably tannish and commonly with small dark paired spots to tip. A lateral stripe, variously fragmented, extends from the loreal area to anterior neck; the preorbital portion is usually sharply

defined (Taylor, 1918; Brown and Alcala, 1978; G. R. Zug [GRZ], personal observation of museum specimens).

China and SEAsia geckos tend to have darker backgrounds than individuals from the Pacific Rim samples. Although Asian geckos have a light phase, the background in this phase is gray to brownish gray. The overall impression of a darker background is heightened by more extensive dorsal and lateral markings in many individuals (Figure 11). Dorsally, the neck and trunk vary from faint reticulations of medium brown through diffuse wavy and brown fragmented crossbars or chevrons to broad, dark brown transverse blotches (usually paired); a moderate pattern seems to be the average condition. Dorsolaterally, a row of light tan to nearly white spots occurs on each side from behind the head to and seemingly forming the anterolateral arms of the postsacral mark. This mark is variable in contrast intensity with the anteromedial dark brown portion, ranging from a large triangular blotch to a moderate transverse bar. The lighter portion of the postsacral mark is typically shades of cream to light yellow. The postsacral mark is broad and deep and extends well on to the tail base; the anterolateral arms are usually weakly developed and short (inconspicuous). The tail is strikingly lighter than trunk with some dark transverse spots or bars (Boulenger, 1903; Bourret, 1937; GRZ, pers. obs. of color images and specimens).

Hong Kong is a geographic outlier from other specimens comprising the China and SEAsia samples. Their coloration differs from the preceding in two major ways. First, the dorsolateral spotting is commonly so faded that it is nearly invisible. The immediate postsacral area is light brown and a median dark edge or bar lies above the vent, and the lighter area is the first band of the diffuse light and dark tail banding (Chan et al., 2006; GRZ, pers. obs. of specimens).

India *H. aurantiacus* is a boldly colored gecko of dark brown bars and blotches on a light to medium brown background (Figure 11A). A dorsal pattern of dark, narrow, wavy crossbars begins on the shoulders and continues to the sacral area; these crossbars can be variously fragmented and/or narrowly connected to anterior or posterior crossbars. A dorsolateral series of light (presumably white to light tan) spots extend from the neck to the inguen; these spots are not evident in all individuals. The tail base pattern is similar to one described above for Hong Kong *Hemiphyllodactylus*. The remainder of the tail is distinctly banded in brown and dark brown; the lighter bands are about twice the width of the dark ones. The loreal area usually has a dark stripe from naris to eye. A dark supraorbital stripe extends from the rear edge of the
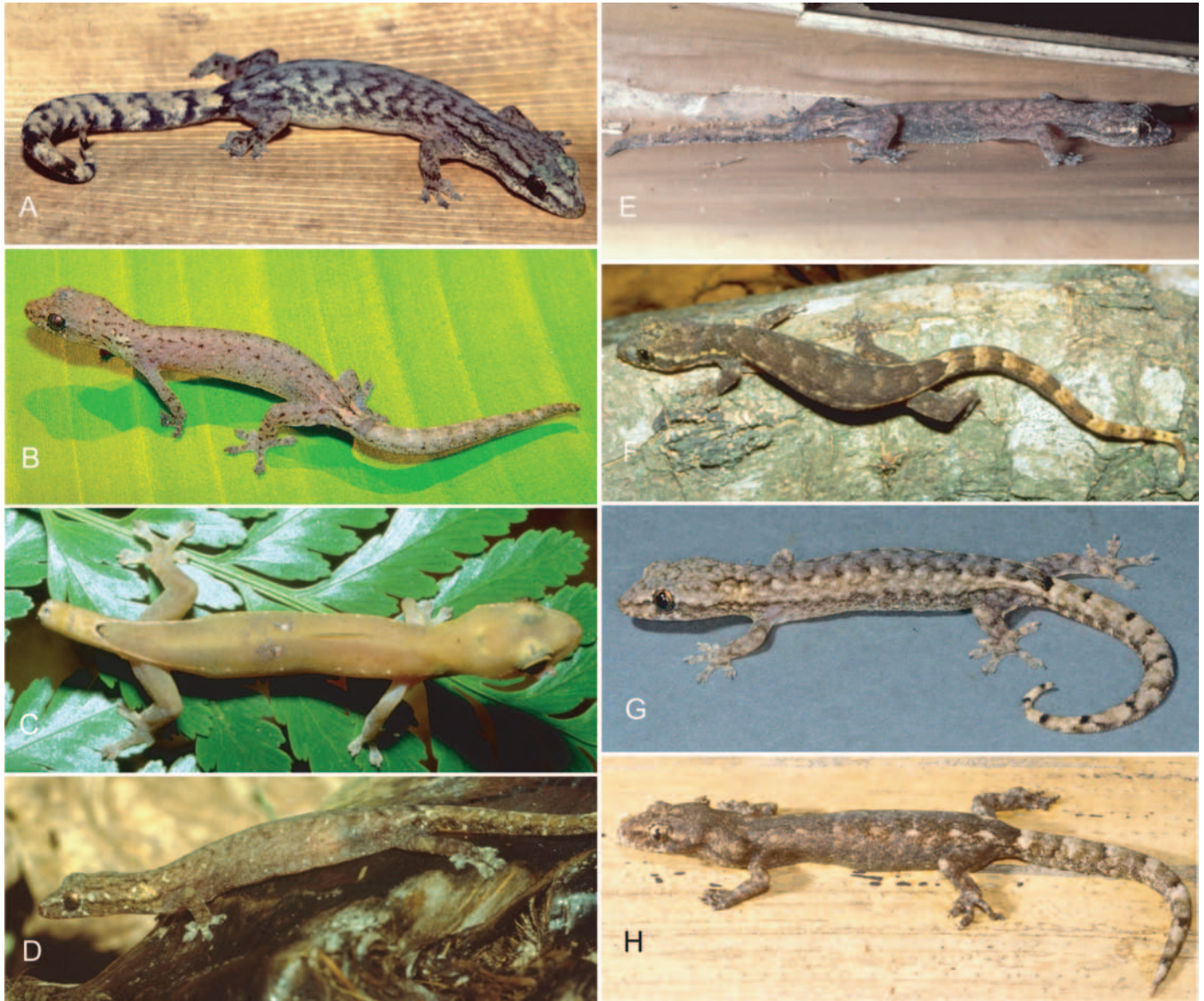
FIGURE 11. Coloration of select *Hemiphyllodactylus* taxa: (A) *H. aurantiacus* (India, Yercaud; AMBauer 5749) (photograph by I. Das); (B), *H. ganoklonis* (Palau; no field/museum number) (photograph by R. I. Crombie); (C) *H. harterti* (Malaysia, Bukit Larut; KUZ 21264) (photograph by H. Ota); (D) *H. typus* (Tonga, ʹEua; USNM 322119) (photograph by G. Zug); (E) *H. typus* (Fiji, Viti Levu; USNM 267978) (photograph by G. Zug); (F) *H. titiwangsaensis* (Malaysia, Cameron Highlands, Tanah Rata; KUZ, no field/museum number) (photograph by H. Ota); (G) *H. yunnanensis* (Thailand, Loei Province; no field/museum number) (photograph by P.-P. van Dijk); (H) *H. yunnanensis* (Myanmar, Pyin Oo Lin; USNM 570734) (photograph by G. Zug).

eye to the anterior trunk. A dark postorbital stripe extends from the eye to the axilla. Both of these stripes are usually unfragmented (Beddome, 1870; Bauer and Das, 1999; GRZ, pers. obs of specimens).

Coloration for the SUNDA gecko "species" cannot be unequivocally resolved with the data at hand. My notes and Boulenger's (1900) description of the *H. larutensis* type are minimal. Its ground color was originally grayish brown, although now (in preserved state) it is faded to light tan. A paired series of small dark spots extend from the neck onto the base of the tail. A few dark spots occur on the sides of the trunk. A dark loreal and a postorbital stripe are present. My notes do not indicate the presence or absence of a dorsolateral series of light spots

or a postsacral mark. Werner's (1900:196) description of *H. harterti* reports "gleicht in Färbung and Zeichnung ganz den *L. lugubris*." I interpret this coloration as a medium brown background with dark wavy crossbars. Photographs (Figure 12) of the type show it faded to near unicolor tan. Brongersma (1931) did not include a description of coloration for *H. margarethae*. Although I examined his type series, I have no notes on their coloration. Presumably, all four type specimens are faded. That is certainly the condition of the two ZMA syntypes photographed (Figure 12).

Excellent color illustrations of Sundan *Hemiphyllodactylus* are available in some recent field guides. Additionally, color photographs were provided by colleagues and an examination of recently preserved specimens from the Malaysian Cameron Highlands. These images and observations allow me to conclude that the three named populations have different colorations.

Manthey and Grossmann (1997, hereinafter M&G) depicted a *H. larutensis* (fig. 172; adult male, Cameron Highlands, Palang, western Malaysia) and a *H. typus* (fig. 173; adult male, Berastagi, northern Sumatra) (In this paragraph, I am using the species identifications provided by the authors for their illustrated specimens.) The same individual (my assumption) of *H. typus* is portrayed in the Cox et al. (1998:85) field guide and in Malkmus et al. (2002: fig. 275). A different individual of M&G's *H. typus* is shown in Chan-ard's et al. (1999:130) (photographic checklist; adult female, Bukit Larut, Perak, Malaysia); another *H. typus* (Chan-ard et al., 1999:130) (adult male, KhaoYai Natl. Park, Nakhon Rachasima, Thailand) is darker. Chan-ard et al. (1999:128–130) also included six images (Cameron Highlands, Malaysia) of *H. larutensis* (Chan-ard's species identification); the male (Chan-ard et al., 1999:130) is the same individual of *H. larutensis* as presented in M&G's field guide. Chan-ard et al. (1999:128) also provided an image of *H. harterti* (adult male, Cameron Highlands). Without specimens available for examination, I cannot confirm the identification of the depicted specimens; nonetheless, a few comments on their specific identification and coloration seem useful although speculative.

First, the Berastagi "*H. typus*" does not have a typical *H. typus* coloration, and, indeed, it is quite striking from other populations described above. Because it lacks the dark dorsal crossbars and the dorsolateral series of light spots, I do not believe the specimen was a *H. typus*. Further, if it was really an adult male, it could not be a *H. typus*, because *H. typus* is a unisexual species. Could it be a *H. margarethae*? Possibly, because it derived from the same mountain range as the latter, although about 3° latitude northward of the Fort de Koch (now Bukittinggi)
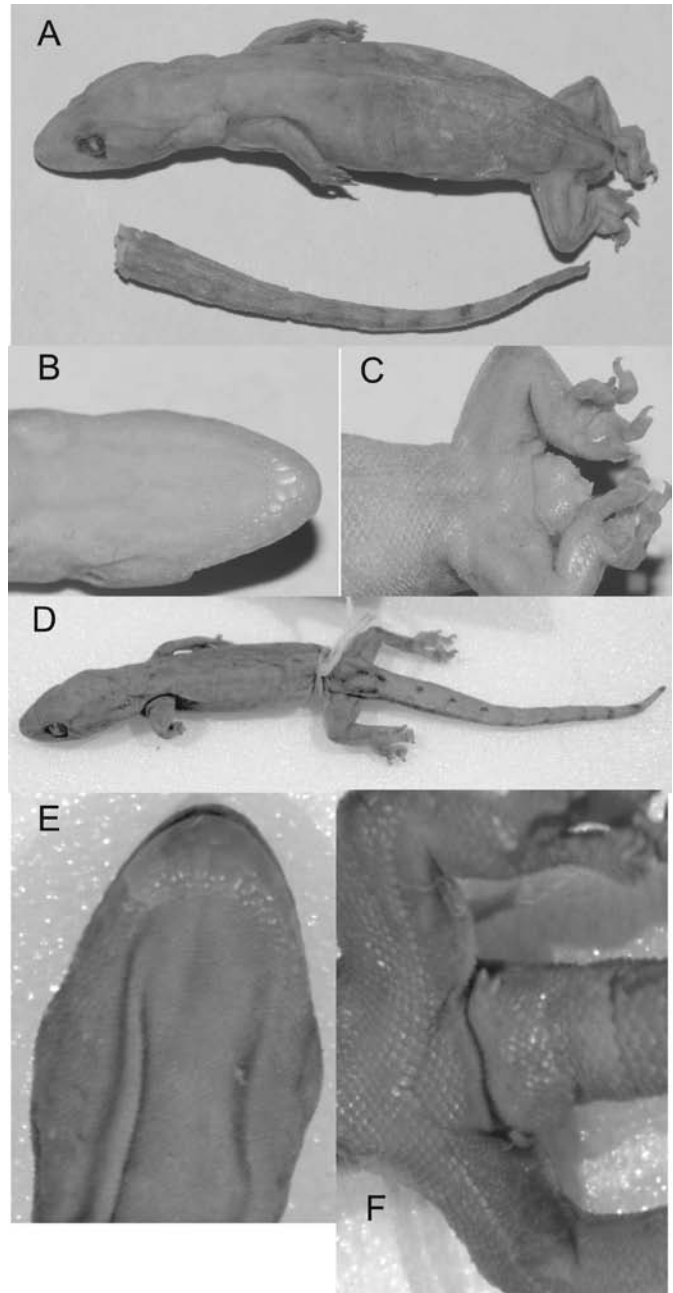
FIGURE 12. Types of Bingtang slender gecko. (**A–C**) *Lepidodactylus Harterti* Werner 1900 (ZMB 15360): (A) dorsal view of whole body, (B) ventral view of throat and chin, and (C) ventral view of pelvic area (photographs by M.-O. Rödel); (**D–F**) *Gehyra larutensis* Boulenger 1900 (BMNH 1901.3.20.2): (D) dorsal view of whole body, (E) ventral view of throat and chin, and (F) ventral view of pelvic area (photographs by G. Zug).

type locality. The two Chan-ard figured *H. typus* possess the near uniform mid-dorsa of the Berastagi one, and the Bukit Larut one has the same overall coloration, although darker, including the continuous dark dorsolateral lateral

stripes and bright anterolateral arms of the postsacral mark of the Berastagi gecko. Chan-ard's Thai *H. typus* has a dorsolateral series of small light spots and well-developed postorbital stripe; nevertheless, I do not believe it is a *H. typus*, owing to light anterolateral arms of a postsacral mark. It is labeled as an adult male and appears to have a hemipenial bulge on the base of the tail. The images labeled *H. harterti* and *H. larutensis* represent individuals from the Cameron Highlands, Malaysia. They do not have the *typus*-style coloration and might represent one or two bisexual species. Certainly, the pattern of several of the specimens is like *Lepidodactylus lugubris*, as noted in Werner's *Lepidodactylus Harterti* description.

Using these images, recent specimens, and colleagues' images, I propose that the coloration of three Sundan populations is distinct for each and offer the following hypotheses. *H. margarethae* is a lightly marked gecko with a striking contrast between body and tail color. The break between the darker trunk and head coloration is at the postsacral "mark." Dorsally, the head and body are a light brown with faded darker brown dorsolateral and lateral stripes. The nape and neck can have a brown mid-dorsal stripe. A light canthal stripe extends from the naris to eye and across the temporal area. The dark postsacral mark is small to absent, but the light arms extend on the posterior trunk. These beige colored arms are continuous with a nearly unicolor tail. (The preceding description was based on Manthey and Grossman, 1997: fig. 173.) Because Larut Hills (Bukit Bintang range) and Cameron Highlands (including Fraser's Hill; both of Banjaran Titiwangsa range) specimens do not share a common coloration in any images available to me, I propose them as separate genetic entities; the former equals *H. harterti* and *H. larutensis*, and the latter represents an unnamed species. *Hemiphyllodactylus harterti* has contrasting body–tail coloration as in *H. margarethae* but is overall darker. The center of the postsacral mark is a narrow dark brown V, which is continuous with a dark brown dorsolateral stripe on each side of the trunk, extending anteriorly to mid neck. The light colored arms (border) extend to above the hips and posteriorly rapidly fade into the unicolor olive of the tail. Light canthal stripes are not evident. (The preceding coloration was based on Chan-ard et al. (1999:130) Bukit Larut "*typus*.") The Titiwangsa gecko is strongly marked. Its background ranges from light tan to olive brown, overlain by a dense dark brown reticulation. This reticulation lacks the regularity of the dark ladder pattern of *Lepidodactylus lugubris*, although it is reminiscent of that pattern. A narrow dark postsacral V with light-colored (to over hips) is usually present. Tail background color generally matches the light color of the

postsacral V; additionally, the tail bears light and dark transverse bars, commonly equal sized. A dorsolateral dark stripe extends from mid-loreal area to axilla. One coloration variant is scattered dark blotches dorsally and laterally on neck and trunk.

PRÉCIS. (1) Although generally drab, bisexual *Hemiphyllodactylus* display some bright markings that seemingly are unique for different populations. (2) Colorful postsacral marks occur in PALAU and PHILIP specimens. The postsacral marks are distinctly U- or V-shaped in the two preceding samples, whereas the dorsolateral arms are weakly developed in most individuals of SEAsia and CHINA. The postsacral mark is the beginning of a lighter (than trunk) tail in Sumatran and Larut Hills individuals and less distinct in Titiwangsa specimens. The postsacral mark for INDIA and Hong Kong geckos is the first contrasting band of the tail.

GEOGRAPHY AND TAXONOMY

REGIONAL PATTERNS OF MORPHOLOGY AND SPECIATION

General Observations

The present study does not address the generic status of the various species currently assigned to the genus *Hemiphyllodactylus*. I recognize the presence of two adult body types among the species currently assigned to this genus (e.g., attenuate body in *Hemiphyllodactylus typus* and robust body in *H. yunnanensis*). I, however, weigh the lamellar morphology of the fore- and hindfeet much more strongly and am comfortable with *Hemiphyllodactylus* as a small monophyletic clade, at least until a robust molecular data set demonstrates otherwise.

Morphological Differentiation

Several morphological features allow the recognition of unique populations (samples) and sets of populations. Foremost among these features is the absence of males in the *Hemiphyllodactylus* populations that are the most geographically widespread. Another striking trait is the presence or absence of gonadal, peritoneal, and caecal pigmentation among both unisexual and bisexual populations. Two body forms are displayed among populations, at least in the older and/or mature individuals. Further, average adult SVL differs among populations, even though size at maturation appears similar among all populations.

Three features of scalation show populational differences. Chin scales in contact with mental and anterior

infralabial scales show two patterns: small (subequal) or slightly larger than the posteriorly adjacent chin scales; or distinctly enlarged with median pair largest (= postmental scales). Secreting precloacal and femoral pores occur consistently in adult females of some *Hemiphyllodactylus* populations and rarely or not at all in other populations. Also, two precloacal–femoral pore arrangements exist (each state uniform within a population): continuous pore series or discontinuous with precloacal pores separated from left and right femoral pores series. In all populations the shape of the digital lamellae is distinctly U- or lyre-shaped. These U-shaped lamellae match Russell's morphological definition (Bergmann and Russell, 2003) of scansors, and they distinctly show a dense microvillous surface as the pad surface dries. The number of lamellae on the digits and hence the digital lamellae formulae varies among populations.

Although these geckos are mostly dull in coloration and this somberness is accentuated by their small size, color and pattern also offer evidence of populational differentiation. The overall dorsal pattern of dark blotches and stripes ranges from nearly nonexistent or diffuse to bold stripes and bars. Intensity and color of the dorsolateral spots varies among populations, as does the presence and coloration of the postsacral mark.

Beginning with reproductive biology, unisexuality is universal among most Pacific-area populations and coastal ones from southern Melanesia through Sunda and Southeast Asia to Sri Lanka. These populations and the Mascarene ones represent the nominate *H. typus*. All these populations share a densely pigmented intestinal caecum, which is frequently visible through the body wall and the pigmentation of the peritoneum covering the gonads and gonadal ducts (specifically the oviducts and epididymides). This pigmentation is not unique to the unisexual populations but also occurs in bisexual ones: Palau, Philip, and India.

I propose that this unique visceral pigmentation (Figure 2) reflects close phylogenetic relatedness among the unisexual *H. typus* and the three bisexual species (justification of the specific status for each Palau, Philip, and India below). I further propose that *H. typus* arose from the hybridization of individuals from the Philippines and Palau. An electrophoretic study (T. D. Schwaner, unpublished data, 1990) examined individuals from northern Thailand (*n* = 13), Philippines (3), Fiji (5), and Hawaii (9) using nine isozymic loci. The Philippine and two Pacific samples share allozymes for all nine loci; although for GPD and IDH, the Philippine sample has two alleles for each of these two isozymes and MPI of the Pacific samples has two alleles. The Thai sample shares alleles

for only three isozyme loci for the Philippine and Pacific samples. The similarity of shared alleles supports the Philippine species as one of the parental species of *H. typus*. Similarities in morphology of Palau and Philippine individuals suggest the former as the other parental species. When and where the hybridization occurred is far more speculative, although a few reasonable conjectures are possible based on the present observations. First, the hybridization event(s) occurred somewhere other than on the parental island groups. *Hemiphyllodactylus typus* occurs infrequently in the Philippine sample and not at all in the Palauan one. Additionally, survival of hybrids without a competitive (numerical) swamping by bisexuals and the opportunity to develop sufficient population density for subsequent dispersal seem more likely to occur off the parental islands than on them. This supposition derives from my observation on rarity of *H. typus* on the islands of the south central Pacific and their rarity on human-made structures in the presence of other gecko species. When other geckos occur with *H. typus*, it occurs in the darkest area, well removed from *Gehyra* and *Lepidodactylus lugubris*, and this segregation occurred before the *Hemidactylus frenatus* invasion of the late twentieth century. Unlike *L. lugubris* in which the unisexuals have displaced the bisexuals to marginal habitats (Ineich, 1999), *H. typus* has not displaced bisexuals or has displaced them only in human habitats. I further speculate that the hybridization event occurred in a location outside the distribution of a bisexual *Hemiphyllodactylus* and likely subsequent to the arrival of humans to the Pacific islands. The preceding origin hypothesis derives from my assumption that the entire distribution of *H. typus* derives from human transport—shipboard, possibly during the eighteenth and early nineteenth centuries.

Phenetic similarities (i.e., primitive advance state polarities not determined) suggest the relatedness of the Palauan and Philippine populations. They share the elongate habitus, small body size (medians, 33 and 35 mm SVL, respectively; Table 3), separated precloacal and femoral pore series, no enlarged chin scales (Table 6), usually two cloacal spurs on each side, and similar coloration traits of a U-shaped postsacral mark and series of small, but bright, spots dorsolaterally on the trunk. Of the preceding traits, the two Pacific bisexual populations share habitus, body size, pore morphology, and chin scale and cloacal spur morphologies with the Indian sample. The presumed hybridization of the Pacific bisexuals yielded a unisexual hybrid (*H. typus* Bleeker) with a larger average body size (>36 mm SVL) but otherwise identical or very similar to the bisexual parental species. *H. typus* is the only

Hemiphyllodactylus taxon in which most (>90%) adult females have secreting precloacal pores. The pores of the unisexual adults appear generally smaller than those of the males of the bisexual taxa. Dorsolateral spots occur in unisexual individuals, although the spots are white to light tan, and the postsacral mark has lost the anterolateral arms.

Even though similar, Palauan and Philippine populations have morphological differences that I interpret to demonstrate speciation. The dorsolateral spots and postsacral mark are red in the Philippine population (*H. insularis* Taylor) in contrast to pink spots and yellow suffused with pink postsacral mark of the Palauan population (unnamed). These two populations also differ in average size, with *H. insularis* slightly larger; more than half the Philip sample exceeds the maximum SVL of Palau specimens. The size distribution of Palau seems unlikely to result from sampling owing to the number of individuals in the sample and the thoroughness, recency, and duration of the Palauan inventory effort (Crombie and Pregill, 1999). Palauan geckos have a proportionately broader head than *H. insularis* ones (65 versus 59% HeadW/HeadL; Table 3, and see also SnW/HeadL therein). In scalation, Palauan geckos average more TotPore than did the Philippine population (27 versus 22.5; Table 6); as noted in the Results section, an increase in TotPore reflects the addition of more femoral pores to the left and right series.

The Indian sample (*H. aurantiacus* Beddome) is a distant geographic outlier to the Pacific *Hemiphyllodactylus* taxa. The Indian geckos also differ strikingly from them by a bolder coloration. The dark transverse dorsal markings are broader and more continuous across the dorsum, and the pre-postorbital stripe is also broader and continuous from naris to shoulder. The postsacral mark is dark yellow to gold and the anterolateral arms are variously developed. The average size of Indian geckos (Table 3) matches that of *H. insularis*, but the relative trunk length (TrunkL/SVL) is shorter (49%) in *H. aurantiacus* than the Pacific taxa (53% Philip, 54% Palau). *H. aurantiacus* has a significantly broader head (76 versus 59 and 65% HeadW/HeadL) than the Pacific taxa, although relative snout width (SnW/HeadL) is the same for all three. The most striking difference of *H. aurantiacus* is its digital lamellae formulae of 2-2-2-2 forefoot and 2-2-3-2 hindfoot. No other population of *Hemiphyllodactylus* has such a low number of lamellae on its digits. The two Sri Lankan non-*typus* specimens examined have very different formulae: 2-2-2-2 and ?-3-3-2 adult male (BMNH 1910.3.16.4); 3-4-4-4 and 5-5-6-5 adult female ([NMB 8552). The male is potentially a *H. aurantiacus*. Its locality data are Hambonota, Ceylon;

however, given that other early BMNH specimens with Ceylon locality data are not members of the Sri Lankan herpetofauna (R. Somaweera, personal communication, March 2007), its status is questionable until a broader sampling of Sri Lankan *Hemiphyllodactylus* is available. The NMB female's locality is only Ceylon; it is possibly a *H. typus* with an unusual hindfoot lamellae formula.

The broader geographic ranges of the eastern Asian samples and prior recognition of multiple taxa makes the resolution of populational and taxonomic boundaries difficult. Bisexual *Hemiphyllodactylus* populations occur from west-central Myanmar (CAS 231030, Chin State) to eastern Guangxi (Zhou et al., 1981: fig. 7). Eastward, a gap of ~1000 km exists from the Guangxi occurrence to the population in the Hong Kong area (Lazell, 2002; Chan et al., 2006). Bisexual populations occur southward from Yunnan-Guangxi through Malayan Peninsula and the Greater Sunda Islands. The occurrence of populations in Indo-China/SE Asia appears very spotty. It is uncertain whether this spottiness is actual occurrence or simply a result of few inventory surveys and/or inadequate vouchering of specimens. I must note that finding *Hemiphyllodactylus* even with intense field surveys is uncommon. For example, in the Pyin-Oo-Lwin area (Myanmar), six researchers inventoried a site multiple times over 2 weeks (mid-monsoon, August 2003) and found only two individuals, one each on two consecutive evenings.

The Chinese populations of *H. yunnanensis* seemingly contrast sharply with the preceding statement of rarity. Late nineteenth century sampling in the Kunming (=Yunnan-fu) area resulted in series of *H. yunnanensis* in many European and North American museums. More recently, Zhou et al. (1981) amassed a collection of 640 specimens of this taxon from nine localities within Yunnan and Guizhou. This number does not indicate rarity within this area and possibly reflects the absences of microsympatry with other geckos, particularly *Hemidactylus* (see Zhao and Adler (1993:304) for list of Yunnan and Guizhou geckos). This abundance also supports the low competitiveness hypothesized for *H. typus* earlier in this section.

Hemiphyllodactylus yunnanensis and the other samples and populations of mainland eastern Asia share the adult robust body form, absence of caecal and gonadal pigmentation, a pair of enlarged postmental chin scales, and a continuous series of precloacal–femoral pores in adult males. The robust morphology (Figure 3) is most apparent in larger individuals and perhaps in adult females, although my measurements and proportions are inadequate to test this proposition. Juveniles and subadults retain a slender trunk, hence a more elongate appearance than adults. The

enlargement of chin scales is more variable within and among populations. None of the eastern Asian populations lack the enlargement of the pair of chin scales abutting the mental scale; however, the degree of enlargement ranges from barely to strongly among populations. The relative enlargement is consistent within each population. Zhou et al. (1981) showed two patterns of postmental enlargement (Figure 7D,E) in their *H. yunnanensis* sample. In their *H. y. yunnanensis*, the postmentals are large with a rapid decrease in size of the arc of chin scales bordering the infralabials; the next arc of chin scales are distinctly smaller and nearly subequal to the remainder of chin scales. The postmentals of *H. y. longlingensis* are moderately large, the infralabial abutting arc of chin scales slightly enlarged as also are the scales in the second arc, inwardly the chin scales quickly become smaller and "typical." Are these two patterns discrete or a continuum? I favor the latter interpretation, although individuals from single-site subsamples that I have examined can usually be assigned to a single state, a few individuals grade into the opposite state. As noted in the Results section, my chin character does not discriminate between the two postmental states of Zhou et al., but all eastern Asian samples share the low count state, including the holotype of *Hemiphyllodactylus typus chapaensis* Bourret. I single out this latter specimen for two reasons: First, Bourret noted small chin scales abutting the mental and infralabials, and his illustration (reproduced in Figure 7F) is ambiguous on this condition; second, if the *chapaensis* population has no enlarged postmental, it differs from the other eastern Asian populations. In this respect, Lazell (2002; also later publications) has identified the Hong Kong population as *H. chapaensis*. Hong Kong geckos match the general eastern Asian morphology, perhaps with a proportionately longer trunk (53 versus <49% for all other Asian subsamples). They have enlarged, although not proportionately larger, postmentals than other Asian mainland population; however, the second arc and some of third arc of chin scales seem proportionately larger than in the other populations. In a contrasting situation, a southern Vietnamese specimen (USNM 146161) has strikingly large postmentals, similar to those depicted for *H. margarethae* in Figure 7C. In contrast, the single southern Cambodian specimen has an arc of small scales.

There is no pattern/differentiation in precloacal–femoral pores visible within the populations and samples from mainland southeastern Asia. These populations share the continuous pattern of precloacal and femoral pore series in contrast to discontinuous pattern of unisexual *H. typus* and the bisexual populations of India, Philippines, and Palau. The continuous pattern continues through the peninsular populations of Thailand and Malaysia. In contrast, the bisexual males of Sumatra and Borneo have discontinuous (separated) pore series.

Taxonomic Decisions and Geography

Which came first, the gecko or the egg? This twisted banality highlights the necessity of addressing the geography of unisexual *Hemiphyllodactylus* separately from that of the bisexual species. Because squamate unisexuality appears to be universally derived from hybridization (Zug et al., 2001), I examine the geographic patterns of occurrence and taxonomy of the bisexual species first.

Among the bisexual species, *H. aurantiacus* (Beddome) was the first to be described and is the easiest of the *Hemiphyllodactylus* populations to be addressed taxonomically. Small adult body size and uniquely low fore- and hindfoot lamellar formulae readily identify it as a distinct genetic entity and phylogenetic lineage. Assuming habitus, visceral pigmentation, and precloacal–femoral pore morphology reflect phylogenetic affinity, *H. aurantiacus* is a member of the *typus* clade.

The two other bisexual members of the *typus* clade are geographically distant—Palau and Philippine islands—from *H. aurantiacus*. Taylor (1918) recognized the distinctiveness of the Philippine populations by several minor differences in scalation from Stejneger's description of *Hemiphyllodactylus leucostictus*. He even noted that it might not be distinct from the latter species, although he highlighted some differences in coloration. Crombie and Pregill (1999) were the first biologists to document the occurrence of *Hemiphyllodactylus* in Palau. Early in their herpetofaunal survey of this island group, they recognized the differentiation of the Palauan population from *H. typus*, first because of the presence of males and second because of its distinct coloration. The latter trait and a few others demonstrate its uniqueness to me, and I describe it as a new species in the following Species Account section.

The bisexual populations of mainland and islands Asia are less readily delimited. This difficulty results largely from inadequate sampling in number of individuals from most localities, too few localities, and localities geographically distant. The uniqueness of *H. yunnanensis* (Boulenger) is unquestionable. Its traits (robust body, unpigmented caeca and gonads, and continuous precloacal–femoral pores) serve to identify a China–Indochina–Sunda clade. I propose that the populations from north central Burma through south central China and the adjacent northern half of Thailand, Laos, and northern Vietnam represent a single taxon *H. yunnanensis*. Some regional populational differentiation occurs in this widely distributed species, although morphological data suggest minimal

genetic differentiation. This hypothesis thus relegates the Zhou et al. subspecies to the synonymy of a monotypic *H. yunnanensis*. *Hemiphyllodactylus typus chapaensis* Bourret similarly becomes a synonym of *H. yunnanensis* (Boulenger). Geographically, the *H. t. chapaensis* type locality is only 300 km south of Kunming (type locality of *H. yunnanensis*) at the southern terminus of a continuous range of mountains. This mountain range also contains the type locality of *H. y. jinpingensis* Zhou et al., and this locality is less than 100 km north of Chapa. Zhou et al. (1981) did not compare the morphology of their samples to *H. t. chapaensis* Bourret.

I noted earlier Lazell's use of *H. chapaensis* for Hong Kong *Hemiphyllodactylus*. This usage must be discontinued because the morphology of the Hong Kong slender geckos is distinct from that of *H. typus chapaensis* Bourret. Does the Hong Kong population represent an outlier of *H. yunnanensis* or is it a unique *Hemiphyllodactylus* population? My present data suggest the latter interpretation, but they are insufficient to address this hypothesis rigorously. Presently, I am unaware of vouchered records of *Hemiphyllodactylus* in Guangxi and Guangdong provinces of southern China. A broad distributional gap also exists for geckos of the *Hemidactylus bowringii* group. Initially, we (Zug et al., 2007) proposed that Hong Kong "*bowringii*" was an exotic species, accidentally introduced from Burma or India. A more detailed study (McMahan and Zug, 2007) subsequently demonstrated the uniqueness of the Hong Kong population. This latter study urges caution, so I am hesitant to postulate the specific status of the Hong Kong *Hemiphyllodactylus* without enlarging my sample and locating vouchers from the Guangxi–Guangdong corridor.

The preceding restriction (in Morphological Differentiation subsection) of *H. yunnanensis* to slender gecko populations from southern China and adjacent northern Indochina leaves the taxonomy of southern Indochina populations unresolved. Again, the inadequacy of museum vouchers does not permit a satisfactory resolution. Presently, the data are adequate to declare that Malay peninsular populations are distinct; however, it is uncertain whether they are confined to the peninsula or extend into southern Indochina, likely the former owing to their restricted occurrence to montane rainforests. The single specimen (USNM 146161) from southern Vietnam suggests this possibility, although morphologically, it appears more similar to the Sumatran population. Also, a sample (THNHM 4910-4917) from Kaeng Krachan National Park, Thailand, just north of the Isthmus of Kra is more similar to other southern Thailand geckos than to Malayan ones. For the present, I recommend labeling southern Indochina and Hong Kong specimens as "*H. yunnanensis.*"

Two names are available for Malayan *Hemiphyllodactylus* populations. *H. larutensis* derives from Bukit Larut (=Maxwell's Hill or Larut Hills), a mountain at the southern end of the Bintang range. Although the type locality of *H. harterti* was given as "Malakka" by Werner (1900), Boulenger (1912) noted that this locality name referred to a general locality and not a specific site (i.e., Malakkahalbinsel [German] equals Malaya [English]). Furthermore, because Ernest Hartert (the donor of the specimen to the Berlin museum) collected birds at Gunong Inas in 1888 (Hartert, 1901–1902; AMNH Department of Ornithology records), Boulenger (1912) tentatively recommended changing the type locality to Gunong Inas. Gunong Inas is ~40 km north of Bukit Larut, and both are mountains within the western Malayan mountain range (Bukit Bintang). I have examined personally only one specimen (*G. larutensis* type) and have data and images from a second specimen (*L. Harterti* type), and there are no traits suggesting that these two represent different taxa. Thus I accept Boulenger's restriction of the type locality to Gunong Inas. I note only that Werner's (1900:196) "gleicht in Färbung und Zeichnung ganz dem *L. lugubris*" better matches the pattern of geckos of the central Malayan mountain range (Bunjaran Titiwangsa); nevertheless, I can find no evidence that Hartert collected in the latter mountain range or received specimens from there. The similarity of morphology of the two type specimens and the type restriction of *H. harterti* to the Bintang range makes *H. harterti* the senior synonym and valid name for the Bintang taxon. The preceding nomenclatural decision results in the populations of Bunjaran Titiwangsa, at least those from the Cameron Highlands southward to the Fraser Hill area, being nameless. These populations have coloration and minor morphological differences from *H. harterti,* their occurrence in a mountain range with a different geological history and long separation by a lowland valley leads me to propose them as a separate phylogenetic lineage.

The sample of Sumatran bisexual geckos is modest but adequate to demonstrate the morphological distinctiveness of these geckos. Thus, in spite of Brongersma's belated change of mind, *H. margarethae* is a unique lineage and presumably Sumatran endemic species. Like *H. harterti* and the central mountain taxon, it appears to be a montane species, confined to cooler and moister habitats than the invasive *H. typus*, whose type locality occurs in Sumatra as well.

I identified most Bornean *Hemiphyllodactylus* specimens as unisexual *typus*. As I analyzed and reexamined my data, I discovered that my identifications resulted in all female specimens as *H. typus* and the three males as unknowns. All Bornean slender geckos have pigmented

caeca; all males have pigmented testes-epididymides peritoneum, all females except one with pigmented oviducal peritoneum. Were my identifications driven by knowledge of sex? The evidence definitely suggests a bias. A reexamination of the specimens is not possible at this stage of the analysis; however, a reexamination of the data suggests that most females were correctly identified as *H. typus*. Tentatively, bisexual individuals can be differentiated from unisexual ones by a higher lamellar formula. The presence of males with normal appearing gonads indicates the presence of a bisexual species as well as the unisexual *H. typus* on Borneo (entire island, not just Indonesian Borneo). Formal recognition of this bisexual species requires a reexamination of all Bornean specimens and comparison with the Philippine *H. insularis*.

Elsewhere in the Sundas, all *Hemiphyllodactylus* are unisexual *typus*. A peculiar situation occurs in Komodo where all individuals are pale, hence Auffenberg's (1980) decision to describe them as a subspecies (*pallidus*) of *H. typus*. Pale *H. typus* are observed elsewhere as one end of a color-phase shift. Because Auffenberg had only two specimens and presumably observed no additional ones, I suggest that by chance he collected and preserved both in their light phase. Presumably, selection for lighter individuals can occur in clonal vertebrates, but the Komodo environment does not seem greatly different from other island habitats with resident populations of *H. typus*.

PHYLOGENY AND BIOGEOGRAPHY: SPECULATIONS. This study was not designed to address phylogenetic relationships within *Hemiphyllodactylus* or its relationships with other gekkonid genera. Morphological similarities and differences among the recognized species taxa led to my hypothesis of two subclades—the *typus* and the *yunnanensis* species groups—and the monophyly of *Hemiphyllodactylus*. Accepting these two items suggests an ancient origin (?Miocene or earlier) of *Hemiphyllodactylus* and an early divergence of the elongate and robust-bodied species groups. Kluge (1968) implicitly proposed *Hemiphyllodactylus* as a member of the *Lepidodactylus* clade, although in his study, he examined nomenclatural issues, not phylogenetic ones. His subsequent studies of gekkonid relationships did not address directly either the interspecific or intergeneric relationships of *Hemiphyllodactylus*. Similarly, this genus has been absent from most other gekkonid phylogenetic studies, although the broad taxon-based studies of A. Bauer and colleagues likely will provide information on the relationships of *Hemiphyllodactylus* and some of the species in this genus. Their initial evaluation (Han et al., 2004) leaves its relationships unresolved.

Having proposed the existence of two sister groups (subclades) of *Hemiphyllodactylus*, I wish to delineate and define these species groups. The *typus* species group contains four, and possibly five, species: *H. typus* Bleeker, *H. aurantiacus* (Beddome), *H. insularis* Taylor, the Palauan population described in the following species accounts, and possibly a fifth, the populations in Borneo. The *yunnanensis* species group contains four, and likely more, species: *H. yunnanensis* (Boulenger), *H. harterti* (Werner), a central Malaysian taxon, *H. margarethae* Brongersma, and possibly a separate species in South China–Hong Kong and southern Indochina. The *typus* species group members have an elongated habitus, accentuated by a long trunk (TrunkL/SVL >50%) with short limbs and proportionately small head, caecum and gonadal ducts darkly pigmented, and precloacal and femoral pore series separated. The *yunnanensis* species group members have a stouter adult habitus although still elongated (TrunkL/SVL ~50%) and proportionately larger head, caecum not pigmented and gonadal ducts rarely so, and precloacal and femoral pore series separated or continuous.

Continuing my speculations on origins and biogeography of the bisexual populations, I suggest that the elongate clade derived from the more robust clade and that its origin occurred in northern precursor-Sunda with dispersal eastward into the Philippines and hence into the western Pacific, and westward to peninsular India, now with only relict populations remaining. *Hemiphyllodactylus aurantiacus* represents a surviving member of this early "dispersal" to India with a long period of isolation. Presently, the situation for the Sri Lankan bisexual population is undecipherable owing to paucity of data. The robust-bodied *Hemiphyllodactylus* has remained and differentiated within the area of the group's origin and northward in southwestern China.

I suggested previously (Morphological Differentiation section) that the origin of the hybrid *H. typus* was an extralimital hybridization of *H. insularis* and the Palauan species. When the hybridization occurred is unknown. A human-induced event seems most likely, as also does an "off the native island" event. The event could have occurred during the early human migrations into and through the Pacific islands or, my preference, with the Euro-American exploration and commercialization of the Pacific. "Off-island" hybridization seems likely owing to presumed low interspecific competitiveness of the unisexual *H. typus* in contrast to the displacement of parental bisexuals by clones of the unisexual *Lepidodactylus lugubris* (Ineich, 1999). I postulate the possibility of onboard ship hybridization then colonization and population expansion in central Pacific. While such an origin could have occurred during the initial human migration into the Pacific, onboard hybridization seems more likely aboard the

larger European sailing ships. Whose ships? The broad distribution and the early occurrence in the Mascarenes hint at an association with French exploration; however, the impact of whaling vessels for the dispersal of Pacific lizards has been overlooked. Whaling vessels were notorious for their catholic (trashy) cargo and for their regular and widespread shore leave. Thus whaling ships provide a "safe-haven" habitat for hybridization and the initial survival of the hybrids; then they could serve for the transfer of hybrids to diverse islands and to other whalers to broaden the dispersal of the hybrids.

Other phylogenetic and biogeographic questions remain for this low diversity taxon. First and foremost is why are there so few species in this gekkonid clade? Its putative sister clade, *Lepidodactylus*, has at least 4 times as many species, and its unisexual species *L. lugubris* (multiple clones, multiple origins) has "outcompeted" its bisexual parent in many Pacific island ecosystems. The *Hemiphyllodactylus* clade displays several distributional anomalies. The widespread occurrence of unisexual *H. typus* contrasts sharply with the bisexual species. In one aspect, this feature is shared with *L. lugubris*, although its low density at most invasive sites differs greatly from mourning gecko occurrences. Also, in contrast to *L. lugubris*, it dispersed more widely. Another peculiarity is the dominance of the stout-bodied *Hemiphyllodactylus* in southeastern Asia and the division of the slender body clade into extreme eastern and western outposts. The stout-bodied geckos show a southern China distributional hiatus, absent from the China–Indochina border then occurring in the Hong Kong area. I earlier noted a similar pattern for the *Hemidactylus bowringii* species group, hence my reluctance to attribute the Hong Kong occurrence to human introduction. The documentation of the distributional patterns of tropical Asian amphibians and reptiles is rudimentary. This situation derives from our poor knowledge of tropical Asian diversity, particularly among mainland taxa, and this poor knowledge results from the continuing recognition of pan-Asian species, when few such species exist (Stuart et al., 2006; Zug, In press).

SPECIES ACCOUNTS

Hemiphyllodactylus typus Bleeker
Indo-Pacific slender gecko

Hemiphyllodactylus typus Bleeker, 1860:327 [type locality: "Agam" (Sumatra); holotype, BMNH 1946.8.30.83].

Platydactylus crepuscularis Bavay, 1869:8 [type locality: "Nouvelle-Calédonie" (locality implied from title of publication); holotype lost (Brygoo, 1990:49)].

Spathodactylus mutilatus Günther, 1872:594 [type locality: "East-Indies archipelago"; holotype, BMNH 1946.8.30.83].

Lepidodactylus ceylonensis Boulenger, 1885:164, Pl. XIII, fig. 3 [type locality: "Gampola" (Ceylon); holotype, BMNH 74.4.29.1326].

Hemiphyllodactylus leucostictus Stejneger, 1899:800 [type locality: "Kauai, Hawaiian Islands"; holotype, USNM 23500].

Hemiphyllodactylus typus pallidus Auffenberg, 1980:72 [type locality: "along Vai Nggulung, Loho Liang, Komodo, 30 mm"; holotype, UF 28985].

Hemiphyllodactylus albostictus Lazell, 1989:126 [spelling error].

COMMENTS.   "Bleeker's types were sold to the British Museum in 1863 (or at least years before 1879, . . .). The type of *H. typus* is the same as that of *Spathodactylus mutilatus* Gthr. (Boulenger l.c.)." The preceding statement is from Brongersma's review (1932:212[footnote 2]) of *Hemiphyllodactylus*.

Taylor's (1963) description of *H. typus* was based on a male from Fraser's Hill, Malaysia. In addition to the specimen being a male, it had a continuous precloacal–femoral pore series; hence the description is not representative of *H. typus*.

DESCRIPTION.   An all-female taxon of geckos (Gekkoninae) with elongate, slender habitus, slightly compressed, elongated appearance accentuated by short limbs and small head (see Figures 3, 6, 13), tail round in cross section and commonly shorter than SVL. Adults 29.4–46.1 mm SVL (mean ± SD, 38.4 mm ± 2.91; n = 143), 14–36 mm TailL (28.5 mm ± 5.03), 15.0–28.0 mm TrunkL (20.3 mm ± 2.11), 6.6–9.9 mm HeadL (8.2 mm ± 0.56), 3.7–6.6 mm HeadW (5.2 mm ± 0.52), 2.3–4.1 mm SnEye (3.4 mm ± 0.30), 1.8–3.4 mm NarEye (2.6 mm ± 0.28), 1.5–2.4 mm EyeD (2.1 mm ± 0.17), 0.9–1.7 mm SnW (1.3 mm ± 0.17). Adult proportions 40–65% TrunkL/SVL (mean ± SD, 52.9% ± 3.2), 18–24% HeadL/SVL (21.3% ± 0.9), 10–16% HeadW/SVL (13.7% ± 1.1), 51–77% HeadW/HeadL (64.1% ± 4.8), 34–48% SnEye/HeadL (41.1% ± 2.4), 24–40% NarEye/HeadL (32.2% ± 2.8), 20–32% EyeD/HeadL (25.3% ± 1.9), 11–21% SnW/HeadL (16.2% ± 1.9), 61–106% EyeD/NarEye (79.0% ± 7.9), 16–34% SnW/HeadW (25.3% ± 3.3).

Scalation predominantly granular from head onto tail, both dorsally and ventrally; ventral trunk scales slightly larger than dorsal ones, 12–19 Dorsal (median ± SD, 15 ± 1.6) and 8–14 Ventral (10 ± 1.3); similarly, subcaudal scales slightly larger than dorsal caudal scales but not plate-like. Cloacal spurs present, modest sized, 1–5 CloacS (2 ± 0.8). Larger scales on lips and snout, rostral largest, rectangular to pentagonal, often slightly concave on dorsomedial edge with slight cleft; 1–5 CircNa (3 ± 0.6), 1–5 SnS (2 ± 0.7); labial scales enlarged from rostral to below eye,

becoming progressively smaller in subocular rictus, 9–14 Suplab (11 ± 1.0), 7–13 Inflab (10 ± 0.9); 9–14 Chin (11 ± 1.1), those behind mental slightly or not enlarged; ear opening distinct with no bordering enlarged scales. Each digit with expanded pad, terminal two phalanges free, arising from within pad on second to fifth digits of fore- and hindfoot and each clawed; pads of these digits each with large triangular apical lamella bordered proximally by lyre-shaped lamellae (scansors); modal digital formulae 3-4-4-4 (forefoot) and 4-4-5-4 (hindfoot) for scansors; first digit of fore- and hindfeet compressed, usually 5 rectangular lamellae (4-5 fore, 5-6 hind) ventrally, terminal phalanx not free with or without minute claw. Adults usually with precloacal pore series (0–14 PreclPor, median ± SD = 10 ± 3.9) always separated from femoral pore series (0–12 combined left and right femoral series), 0–26 TotPore (12 ± 7.2).

Dusky tan to reddish brown ground color dorsally and laterally from head to tail, usually with dark ocular stripe from loreal area to anterior trunk; series of widely spaced small white spots, often darkly edged, dorsolaterally from temporal area to inguina; dorsal postsacral dark brown blotch bordered posteriorly by transverse bar of white or beige. Underside dusky from chin to vent, pale yellowish orange on tail.

Major diagnostic features are as follows: all-female taxon; pigmented caecum and gonadal ducts; if present (uncommonly), femoral pore series separate from precloacal pore series; chin scales bordering mental and first infralabial not greatly enlarged; digital lamellae formulae 3-4-4-4 (forefoot) and 4-4-5-4 (hindfoot); average adult SVL ~38 mm; series of white spots dorsolaterally on trunk and bright postsacral bar of white and dark brown.

Description of holotype: An adult female (Figure 13), 43.3 mm SVL, 40.0 mm TailL, 22.4 mm TrunkL, 9.1 mm HeadL, 5.8 mm HeadW, 3.7 mm SnEye, 2.9 mm NarEye, 2.1 mm EyeD, and 1.1 mm SnW. Proportions: 52% TrunkL/SVL, 21% HeadL/SVL, 13% HeadW/SVL, 64% HeadW/HeadL, 41% SnEye/HeadL, 32% NarEye/HeadL, 23% EyeD/HeadL, 12% SnW/HeadL, 72% EyeD/NarEye, 19% SnW/HeadW. Scalation: 3 CircNa, 3 SnS, 11 Suplab, 11 Inflab, 13 Chin (anteromedial ones only slightly larger than adjacent ones), 13 Dorsal, 8 Ventral, 2 CloacS, Subcaud not enlarged, 15 PreclPor, 23 TotPore with no contact between precloacal and femoral, digital formulae 3-3-4-3 fore and 3-4-4-4 hind. Pigmented caecum, pigmentation unknown for oviducts.

Body ground color faded to a uniform orangish tan, no lateral spotting evident, dark lateral stripe from in front of eye to axilla, broken dark reticulations on rear of head and nape, dark chevron at tail base.
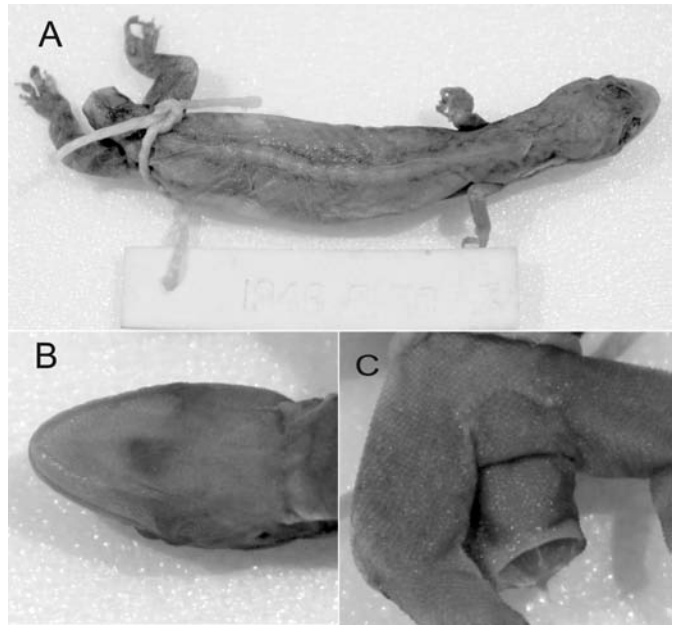

FIGURE 13. Holotype of *Hemiphyllodactylus typus* Bleeker, 1860 (BMNH 1946.8.30.83): (A) dorsal view of whole body, (B) ventral view of throat and chin, and (C) ventral view of pelvic area.

ETYMOLOGY. Bleeker offered no explanation of his selection of the name *typus*. The name is a Latin noun for impression, shape, Figure, or example. I assume that he chose *typus* because this species represented the type species for his new genus *Hemiphyllodactylus*.

I propose a standard English name at variance to the commonly used Indo-Pacific tree gecko. Whereas this gecko is occasionally found on trees, it more commonly occurs in the leaf whorls of *Pandanus* and on human-made structures. Slender refers to the elongate and attenuate appearance of *H. typus* and most of its congeners.

VARIATION. The means or medians and ranges are detailed in the preceding Description section. No significant or striking variation was seen in any of the characters among the samples from throughout the range of this taxon. The variation observed within each character is equivalent to that observed in the repeated measures data of a Palauan bisexual female. Where character variation is greater, the variation is likely attributed to data-gathering variance arising from the poor preservation quality of many specimens. I suggest that this low variation among the widely separated population is evidence that all populations of *H. typus* derive from a single hybridization event and subsequent dispersal of this single clonal

population. The lightness of Auffenberg's Komodo specimens is attributed to chance.

DISTRIBUTION.   Broadly, if somewhat spottily, distributed from Hawaii and French Polynesia in the central Pacific westward to Pacific Rim islands and coastally through New Guinea, Sunda, and Indochina to Sri Lanka; also occurs in Mascarene Islands (Figure 14).

Hemiphyllodactylus aurantiacus Beddome
Southern Ghats slender gecko

Hemidactylus aurantiacus Beddome, 1870:33 [Type locality: "Shevaroys, under stones about Yercaud and elsewhere at an elevation of 4000 feet" (Tamil Nuda, India); syntypes: BMNH 74.4.29.1332–1337, ZMB 10233; lectotype, BMNH 74.4.29.1333].

COMMENTS.   Beddome's description is ambiguous on the number of specimens available to him as he composed the description. His description is based on a single specimen (~30–31 mm SVL), presumably immature, sex uncertain (no precloacal pores). The syntypic series (BMNH 74.429.1332–1337) consists of nine individuals, two adult males, three females (all with adult SVLs but two with immature ovaries), and four juveniles. I designate the male BMNH 74.429.1333 as the lectotype of *Hemidactylus aurantiacus* Beddome, owing to my reluctance to use an immature specimen as a type and the absence of an immature specimen matching Beddome's dimensions. Additionally, I accept Bauer and Günther's (1991) assessment that ZMB 10233 is a syntype; it is a mature male (32-mm SVL) with precloacal and femoral pores, hence also not the specimen on which Beddome based his description.

DESCRIPTION.   A bisexual taxon of geckos (Gekkoninae) with elongate, slender habitus, slightly compressed, elongated appearance accentuated by short limbs and modest head (see Figures 3, 11, 15), tail somewhat elliptical in cross section and regularly shorter than SVL. Adults 27.2–37.9 mm SVL (mean ± SD, 34.3 mm ± 2.80; n = 14), 26–33 mm TailL (29.2 mm ± 2.87), 13.8–18.8 mm TrunkL (16.7 mm ± 1.27), 6.0–8.7 mm HeadL (7.9 mm ± 0.64), 4.3–6.5 mm HeadW (5.6 mm ± 0.72), 2.3–3.7 mm SnEye (3.1 mm ± 0.36), 1.9–2.8 mm NarEye (2.4 mm ± 0.25), 1.7–2.1 mm EyeD (2.0 mm ± 0.13), 1.2–1.5 mm SnW (1.3 mm ± 0.10). Adult proportions 44–51% TrunkL/SVL (mean ± SD, 48.7% ± 2.0), 21–26% HeadL/SVL (23.0% ± 1.0), 14–19% HeadW/SVL (16.5% ± 2.9), 57–79% HeadW/HeadL (71.3% ± 7.1), 34–42% SnEye/HeadL (39.2% ± 2.6), 27–33% NarEye/HeadL (30.6% ± 1.8), 22–28% EyeD/HeadL (25.0% ± 1.7), 14–20% SnW/HeadL (16.7% ± 1.4), 69–96% EyeD/NarEye (82.0% ± 7.7), 21–30% SnW/HeadW (23.5% ± 2.7%).

Scalation is predominantly granular from head onto tail, both dorsally and ventrally; ventral trunk scales slightly larger than dorsal ones, 11–17 Dorsal (median ± SD, 13.0 ± 1.87) and 8–12 Ventral (10.0 ± 1.51); similarly, subcaudal scales slightly larger than dorsal caudal scales but not plate-like. Cloacal spurs present, modest sized, 1–3 CloacS (2 ± 0.6). Larger scales on lips and snout, rostral largest, rectangular to pentagonal, often slightly concave on dorsomedial edge with slight cleft; 2–4 CircNa (3 ± 0.5), 3–6 SnS (4 ± 0.9); labial scales enlarged from rostral to below eye, becoming progressively smaller in subocular rictus, 10–13 Suplab (10 ± 1.0), 8–12 Inflab (11 ± 1.0); 10–14 Chin (11 ± 0.8), those behind mental slightly or not enlarged; ear opening distinct with no bordering enlarged scales. Each digit with expanded pad, terminal two phalanges free, arising from within pad on second to fifth digits of fore- and hindfoot and each clawed; pads of these digits each with large triangular apical lamella bordered proximally by lyre-shaped lamellae (scansors); modal digital formulae 2-2-2-2 (forefoot) and 2-2-3-2 or 3 (hindfoot) for scansors; first digit of fore- and hindfeet compressed, usually 4 rectangular lamellae (3-4 fore, 4-5 hind) ventrally, terminal phalanx not free with or without minute claw. Adult females rarely with precloacal pore series (0–3 PreclPor), males always with precloacal pores (median ± SD, 7 ± 1.6; range, 6–11) always separated from femoral pore series, 16–25 TotPore (21.5 ± 2.92).

Dusky brown ground color dorsally and laterally from head to tail, dark ocular stripe from loreal area to axilla thereafter interrupted and part of zigzag dorsal markings; also narrow dorsolateral dark stripe from rear of eye to axilla, where it also breaks into pieces of the dorsal zigzag marks; small white spots dorsolaterally on trunk but overwhelmed by dark trunk markings; dorsal postsacral mark, anteriormost broad dark brown traverse bar bordered behind by light golden bar then tan and subsequently by irregular edged dark brown bars separated by tan interspaces.

Major diagnostic features are as follows: bisexual taxon; pigmented caecum and gonadal ducts; in adult males femoral pore series separated from precloacal pore series (TotPore typically ≥20-≤25), always absent in females; chin scales bordering mental and first infralabial not greatly enlarged; digital lamellae formulae 2-2-2-2 (forefoot) and 2-2-3-2 or 2-2-3-3 (hindfoot); average adult SVL ~33–35 mm; bold body pattern of contrasting dark brown and dusky brown background and dorsal postsacral double bar of dark brown and light orange (Figure 15).
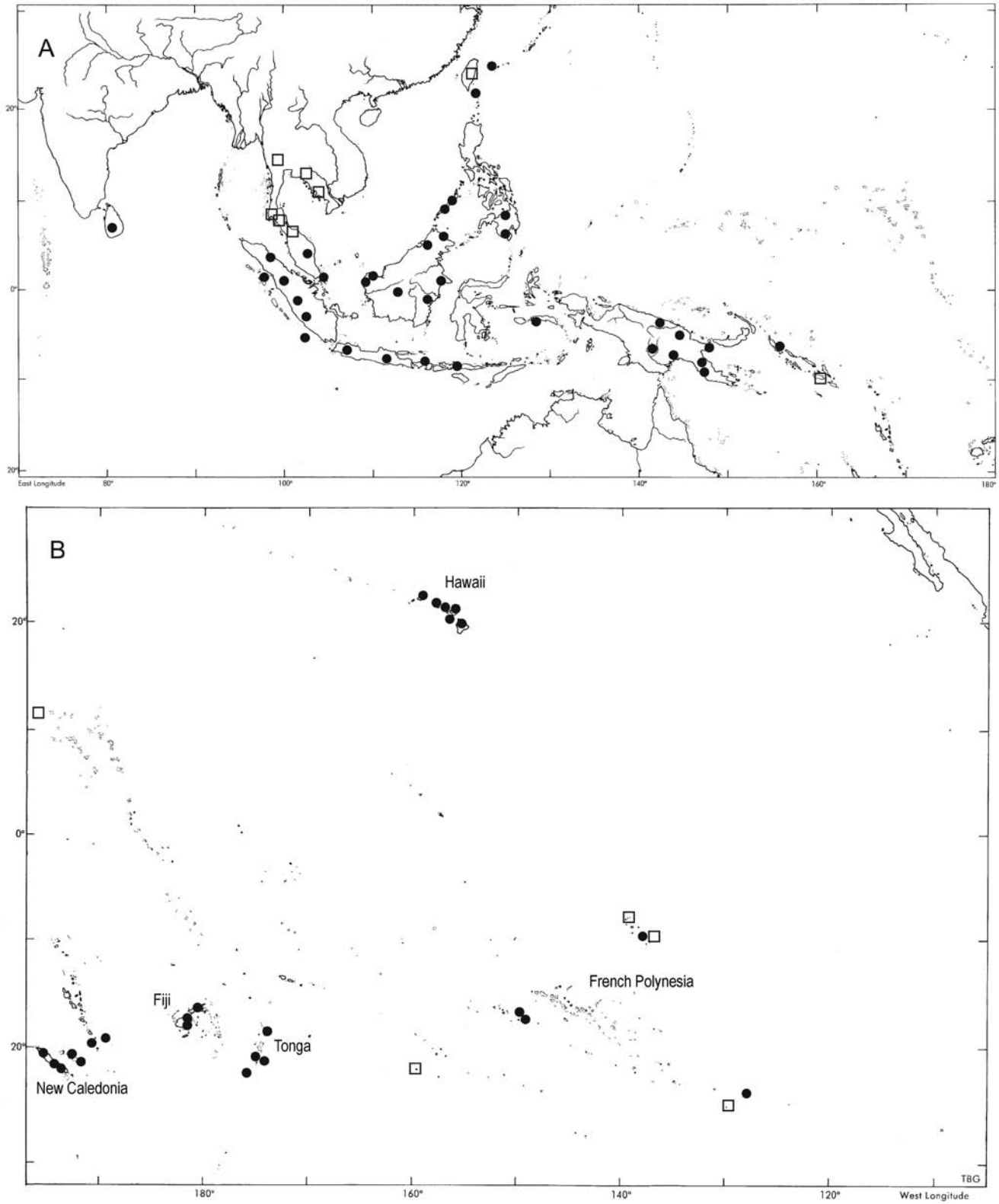
FIGURE 14. Geographic occurrence of *Hemiphyllodactylus typus*. Not all localities in the same area are plotted. (A) Asia records [Asia and Islands] and (B) Oceania records. Symbols: solid circle = specimen(s) represented by museum vouchers and specific identity confirmed; open square = locality from published records or museum records but specimen not examined.
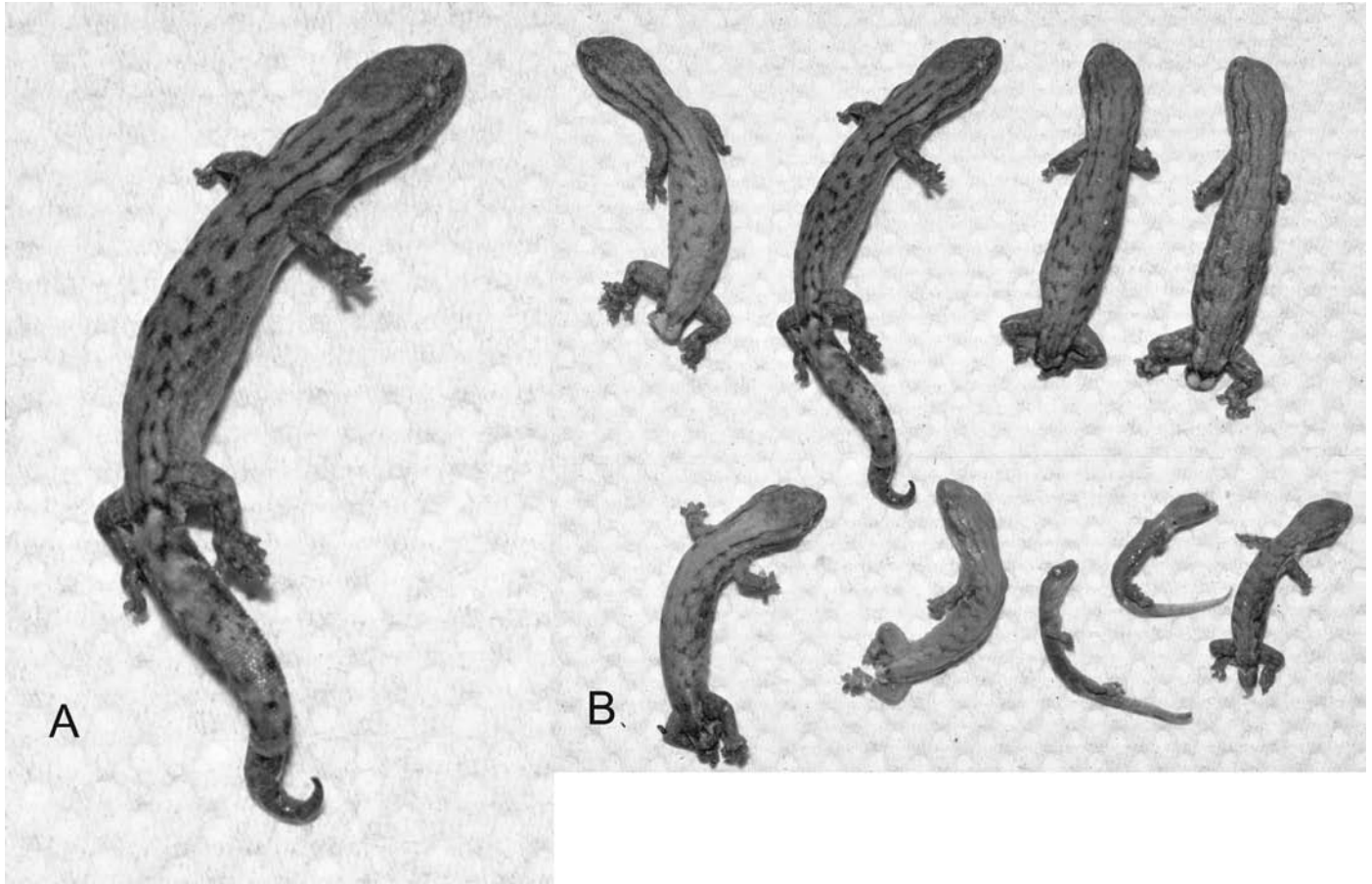
FIGURE 15. Syntypes of *Hemiphyllodactylus aurantiacus* Beddome, 1870: (A) lectotype (BMNH 74.4.29.1333) and (B) syntypic series (from top row, left to right, BMNH 74.4.29.1332–1337 and three unnumbered juveniles). (Photographs by G. Zug.)

Description of lectotype: An adult male: 34.5 mm SVL, broken TailL, 17.5 mm TrunkL, 7.8 mm HeadL, 5.6 mm HeadW, 3.7 mm SnEye, 2.8 mm NarEye, 2.0 mm EyeD, and 1.2 mm SnW. Proportions: 51% TrunkL/SVL, 23% HeadL/SVL, 16% HeadW/SVL, 72% HeadW/HeadL, 40% SnEye/HeadL, 30% NarEye/HeadL, 26% EyeD/HeadL, 15% SnW/HeadL, 87% EyeD/NarEye, 21% SnW/HeadW. Scalation: 3 CircNa, 5 SnS, 13 Suplab, 11 Inflab, 12 Chin (anteromedial ones only slightly larger than adjacent ones), 16 Dorsal, 12 Ventral, 1 CloacS, Subcaud not enlarged, 7 PreclPor, 22 TotPore with no contact between precloacal and femoral, digital formulae 2-2-2-2 (forefoot) and 2-3-3-3 (hindfoot). Pigmented caecum, pigmentation unknown for testis epididymis.

Body ground color brown, no lateral light spotting evident, dark dorsolateral stripe from eye to shoulder, lateral stripe from in front of eye to axilla, these stripes broken on trunk and form lateral parts of dorsal chevron or zigzag markings of trunk, dark chevron at tail base.

ETYMOLOGY. Beddome offered no explanation for his choice of *aurantiacus* as the epithet for his new species. He did mention the orange color of the tail base, and because *aurantium* is a new Latin noun for the orange (fruit), I suggest his choice derived from the association between the color of the orange and the gecko's tail.

VARIATION. The means or medians and ranges are detailed in the preceding Description subsection. Males are somewhat smaller than females, but the difference in average size is slight and not statistically significant. None of the mensural traits shows significant sexual dimorphism and neither do any meristic traits other than precloacal and femoral pores. One large female possesses three secreting precloacal pores; no other females have secreting pores. All adult males possess both precloacal and femoral pore series.

DISTRIBUTION. This gecko is an endemic of the southern tip of India (Tamil Nadu) (Figure 16). It occurs mainly in association with evergreen forest at
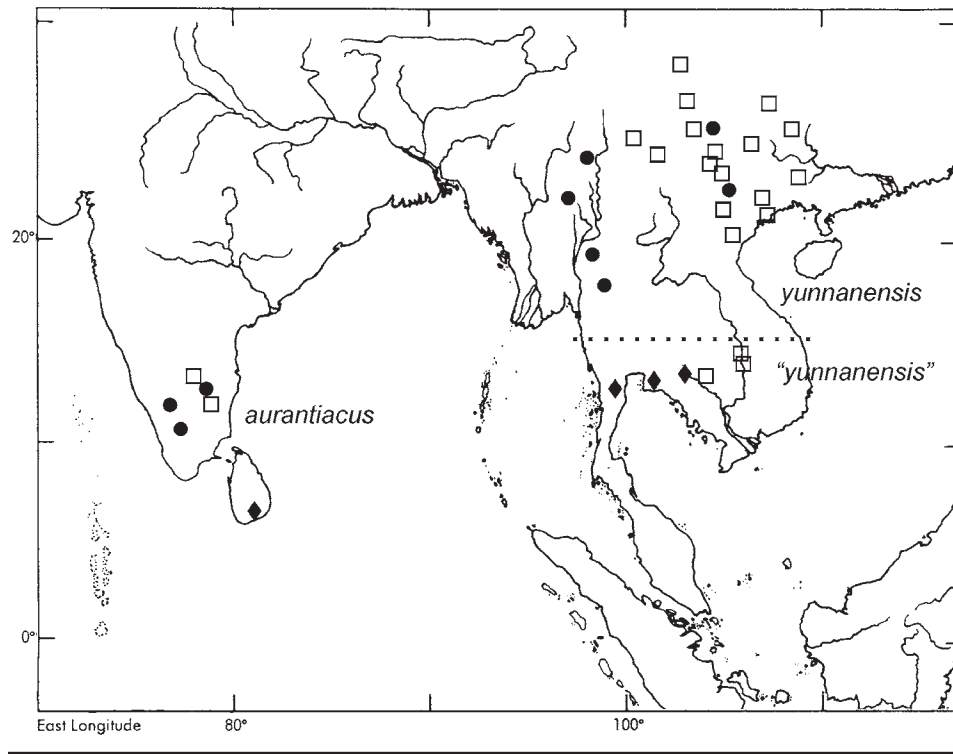
FIGURE 16. Geographic occurrence of *Hemiphyllodactylus aurantiacus* and *H. yunnanensis*. Not all localities in the same area are plotted. Symbols: circle, specimens represented by museum vouchers and specific identity confirmed; square, localities from published records or museum records but specimen not examined; diamond or square below mid-Indochina boundary (dotted line), specimens and records tentatively assigned to *H. yunnanensis*.

mid-elevations in the Nilgiri and Anaimalai Hills (Western Ghats) and Shevaroy and Kolli Hills (Eastern Ghats). Its occurrence in Banglore is edificarian and appears to represent a recent accidental transport. (Distributional summary largely from Bauer and Das, 1999.)

Hemiphyllodactylus ganoklonis Zug, new species
Palauan slender gecko

HOLOTYPE. USNM 563682, adult male from Palau Islands, extreme northern tip of Ulebsechel Island, 50 m south of channel between Ngermalk and Ulebsechel, collected by Ronald I. Crombie, 2 August 1998.

PARATYPES. All subsequent specimens are from Republic of Palau (= Palau Islands); that datum is removed from each subsequent locality for brevity. SAM R47715, Babeldaob Island, 4 mi [6.4 km] north on west coast road to Aimeliik, 7°24′N 134°30′E, collected by Christopher C. Austin, 2 June 1996. USNM 495065,

Babeldaob Island, east of Nekkeng, 0.5 km west of Tabecheding River (Aimeliik State) 7°27′25″N 134°30′40″E, collected by Gordon H. Rodda, 17 January 1993; USNM 495066, Babeldaob Island, 1 km east of Ngerchaech Mountain, Koksai Radio Station (Ngetpang State) 25 m 7°26′42″N 134°31′48″E, collected by Gordon H. Rodda and Renee J. Rondeau, 18 January 1993; USNM 563663, Babeldaob Island, access road to Palau airport, near turnoff into airport itself (Airai State), collected by Ronald I. Crombie and Christopher C. Austin, 7 July 1996; USNM 563664–665, Babeldaob Island, just north of Ulimang village on road to Galap village (Ngaraard State), collected by Ronald I. Crombie and Gregory K. Pregill, 14 January 1995; USNM 563666, Babeldaob Island, south of Ulimang village (Ngaraard State), collected by Ronald I. Crombie, 6 April 1995; USNM 563667, Ngeanges Island, 7°12′26″N 134°22′21″E, collected by Ronald I. Crombie, 9 January 1998; USNM 563668, Ngeaur Island, Ngaramasch village, collected by Ronald I. Crombie, Gregory K. Pregill, and G. Ken Creighton, 30 January

1993; USNM 563669–71, Ngercheu Island group, Carp Island, 7°05′36″N 134°16′44″E, collected by Ronald I. Crombie, 18 July 2001; USNM 563672–673 same as preceding, except 13 August 2001; USNM 563674 same as preceding, except 15 August 2001; USNM 563675 Ngerekebesang Island, southwest (by road) of Meyungs village, just northeast of turnoff to Echang village, collected by Ronald I. Crombie and Gregory K. Pregill, 9 June 1994; USNM 563676 Ngerektabel Island, approx. 0.5 km (air) northwest of Rael Di, at a sandy beach labelled Oimaderuul on topographic map, collected by Ronald I. Crombie, 4 August 1998; USNM 563677, Oreor Island, southwest of Ngermid village at Ngerunguikl, Hotel Nikko Palau, collected by Ronald I. Crombie, 22 April 1992; USNM 563678, Ulebsechel Island, Snake Dick Point, midpoint of east coast, 7°19′19″N 134°29′15″E, collected by Ronald I. Crombie and Artemio B. Asis, 28 December 1997; USNM 563679–681, Ulebsechel Island, same data as holotype; USNM 563683, Ulebsechel Island, same data as holotype, except 12 February 2002.

Adult females: USNM 495066, 563663–664, -666– 667, -672–673, -675, -679, -681, -684; adult males: SAM R47713, USNM 495065, 563665, -668–671, -674, -676, -678, -682; juveniles: USNM 563677.

DESCRIPTION.   A bisexual taxon of geckos (Gekkoninae) with elongate, slender habitus, slightly compressed, elongated appearance accentuated by short limbs and small head (see Figures 3, 11, 17, 18), tail round in cross section and usually shorter than SVL. Adults dimorphic, females larger than males: 31.1–34.2 mm (mean ± SD, 32.8 ± 1.01; n = 11 females), 28.3–31.6 mm (30.3 mm ± 1.11, n = 12 males) SVL; TailL ~2/3–3/4 of SVL; 16.8– 18.9 mm (17.8 mm ± 0.76), 14.4–17.4 mm (16.0 mm ± 0.95) TrunkL; 6.6–7.5 mm (7.1 mm ± 0.26), 6.3–7.0 mm (6.7 mm ± 0.24) HeadL; 3.8–4.4 mm (4.2 mm ± 0.17), 3.5–4.1 mm (3.8 mm ± 0.20) HeadW; 2.6–3.1 mm (2.8 mm ± 0.16), 2.4–3.0 mm (2.6 mm ± 0.18) SnEye; 2.1–2.3 mm (2.2 mm ± 0.09), 1.8–2.3 mm (2.1 mm ± 0.17) NarEye; 1.7–1.9 mm (1.8 mm ± 0.09), 1.5–1.9 mm (1.7 mm ± 0.15) EyeD; 1.0–1.3 mm (1.1 mm ± 0.11), 1.0–1.1 mm (1.0 mm ± 0.05) SnW. Adult proportions not dimorphic, 49–57% TrunkL/SVL (mean % ± SD, 53.5% ± 2.3), 20–23% HeadL/ SVL (21.8% ± 0.6), 12–15% HeadW/SVL (12.6% ± 0.7), 53–65% HeadW/HeadL (58.0% ± 3.2), 36–45% SnEye/ HeadL (39.2% ± 2.0), 28–34% NarEye/HeadL (31.0% ± 1.4), 23–28% EyeD/HeadL (25.5% ± 1.5), 13–19% SnW/ HeadL (15.6% ± 1.2), 73–95% EyeD/NarEye (82.4% ± 5.6), 23–32% SnW/HeadW (27.0% ± 2.0%).

Scalation is predominantly granular from head onto tail, both dorsally and ventrally; ventral trunk scales slightly

FIGURE 17. *Hemiphyllodactylus ganoklonis* from Ulebsechel Island, Palau (USNM 563680). (Illustration by M. D. Griffin.)

larger than dorsal ones, 11–18 Dorsal (median ± SD, 15 ± 1.4) and 9–12 Ventral (10 ± 1.0); similarly, subcaudal scales slightly larger than dorsal caudal scales but not plate-like. Cloacal spurs present, modest sized, 1–4 CloacS (2 ± 1.0). Larger scales on lips and snout, rostral largest, rectangular to pentagonal, often slightly concave on dorsomedial edge with slight cleft; 2–4 CircNa (3 ± 0.6), 3–5 SnS (4 ± 0.7); labial scales enlarged from rostral to below eye, becoming progressively smaller in subocular rictus, 8–11 Suplab

(8 ± 0.8), 8–10 Inflab (9 ± 0.6); 9–12 Chin (11 ± 0.9), those behind mental slightly or not enlarged; ear opening distinct with no bordering enlarged scales. Each digit with expanded pad, terminal two phalanges free, arising from within pad on second to fifth digits of fore- and hindfoot and each clawed; pads of these digits each with large triangular apical lamella bordered proximally by lyre-shaped lamellae (scansors); modal digital formulae 3-4-4-3 (forefoot) and 3-4-4-4 (hindfoot) for scansors; first digit of fore- and hindfeet compressed, usually 4 rectangular lamellae (3-5 fore, 3-5 hind) ventrally, terminal phalanx not free with or without minute claw. Adult females lack precloacal pore series, males always with precloacal pores (median ± SD, 8 ± 0.9; range, 6–9) always separated from femoral pore series, 16–28 TotPore (22.5 ± 4.01).

In life, light dusky tan to reddish beige ground color dorsally and laterally from head to hips, narrow dark brown ocular stripe on posterior edge of loreal area and continuing behind eye either slightly or to edge of temporal region (jowl), a narrow dark lateral stripe on neck broken and reduced to complete stripe, no dark lateral stripe but in some individuals widely spaced series of dark spots or lines; dorsally on head some dark brown bilateral spotting, continuing onto trunk as parasagittal row of small dark marks; dorsolateral series of yellow spots on each side from jowl to anterior arm of postsacral mark; bright postsacral mark with middorsal dark brown spot bordered behind and laterally by light orange to pinkish yellow V, arms of which extending to posterior edge of abdomen. Tail distinctly lighter (yellowish) than trunk, widely spaced narrow orangish rings and middorsal diffuse dark spots in brown interspaces. Venter similar to dorsal ground color, a shade lighter; underside of tail light to bold yellow.

In alcohol, pattern same as above, generally ground color darker from light to medium brown; dark stripes and other markings remain distinct, lighter marks lose color becoming white to light tan, including the orange border of postsacral mark; venter strikingly lighter than dorsum, retaining a dusky appearance owing to one or two small brown spots in most ventral scales.

Major diagnostic features are as follows: bisexual taxon; pigmented caecum and gonadal ducts; in adult males femoral pore series separate from precloacal pore series, absent in females; chin scales bordering mental and first infralabial not greatly enlarged; digital lamellae formulae usually 3-4-4-3 (forefoot) and 3-4-4-4 (hindfoot); average adult SVL ~31–32 mm; mute coloration of light brown background with small scattering of dark brown spots, contrasting with a bright postsacral marking with small dark brown center with light orange V-shaped border and series of widely spaced dorsolateral orange spots.

Description of holotype: An adult male (Figure 18), 31.2 mm SVL, 23 mm TailL (regenerated), 16.9 mm TrunkL, 7.0 mm HeadL, 4.0 mm HeadW, 2.8 mm SnEye, 1.9 mm NarEye, 1.7 mm EyeD, and 1.2 mm SnW. Proportions: 53% TrunkL/SVL, 22% HeadL/SVL, 12% HeadW/SVL, 57% HeadW/HeadL, 38% SnEye/HeadL, 30% NarEye/HeadL, 25% EyeD/HeadL, 16% SnW/HeadL, 84% EyeD/NarEye, 28% SnW/HeadW. Scalation: 3 CircNa, 5 SnS, 8 Suplab, 9 Inflab, 12 Chin (anteromedial ones only slightly larger than adjacent ones), 16 Dorsal, 11 Ventral, 4 CloacS, Subcaud not enlarged, 9 PreclPor, 25 TotPore with
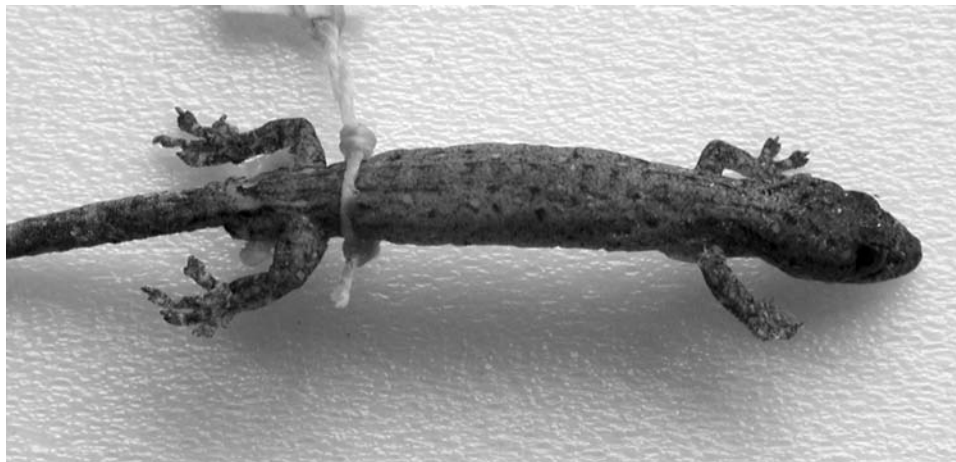

FIGURE 18. Holotype of *Hemiphyllodactylus ganoklonis* (USNM 563682) from Ulebsechel Island, Palau. (Photograph by G. Zug.)

no contact between precloacal and femoral, digital formulae 3-4-4-4 forefoot and 4-4-5-4 hindfoot. Pigmented caecum, testes lightly pigmented, no pigment on anterior portion of epididymis, heavily pigmented posterior two-thirds.

In alcohol, body ground color light brown with medium to dark brown markings, dorsolateral light spotting from eye to inguina (4 between eye and axilla, 9 between axilla and inguina (right side), partial dark dorsolateral stripe from eye to neck, no lateral stripes elsewhere, series of widely spaced small dark dashes and spots parasagittally and fewer laterally, postsacral dark brown chevron middorsally at tail base edged laterally by broad white border. Tail background slightly darker than trunk with widely scattered dark flecks. Ventrally dusky cream from chin to vent because many ventral scales with central dark spot.

ETYMOLOGY.   The name *ganoklonis* derives from the Greek adjective and noun, *ganos* for bright or brightness and *klonis* for buttock or rump. The bright rump refers to the bright yellow chevron (postsacral) mark at the base of the tail. The name is proposed as an adjective.

VARIATION.   The means or medians and ranges are detailed in the preceding Description section. *Hemiphyllodactylus ganoklonis* is the smallest *Hemiphyllodactylus* taxon, yet it possesses a slight, but significant, size dimorphism with females averaging 2 mm larger than males. This larger size in females also is reflected in other mensural traits: TrunkL, HeadL, HeadW, NarEye, and EyeD. Body proportions and scalation are not dimorphic.

Overall, variation within each trait is low and often the lowest of all regional samples. This low variation reflects the high quality of preservation of the Palauan sample and is not due to a limited geographic sampling. The Palauan sample derives from seven different islands and multiple sites on a few islands.

DISTRIBUTION.   *Hemiphyllodactylus ganoklonis* occurs throughout the major islands of Palau (Figure 19).

Hemiphyllodactylus harterti Werner
Bintang slender gecko

Lepidodactylus Harterti Werner, 1900:196 [type locality: "Malakka" (Malaysia), restricted to "Gunong Inas" (Perak, Malaysia); holotype, ZMB 15360].

Gehyra larutensis Boulenger, 1900:188 [type locality: "Larut Hills, . . . , at 3500 feet altitude" (Malaysia); holotype, BMNH 1901.3.20.2].

COMMENT.   The type locality of *H. harterti* was tentatively restricted by Boulenger in a footnote (1912: 48): "Dr. Hartert collected on Gunong Inas, the type locality of
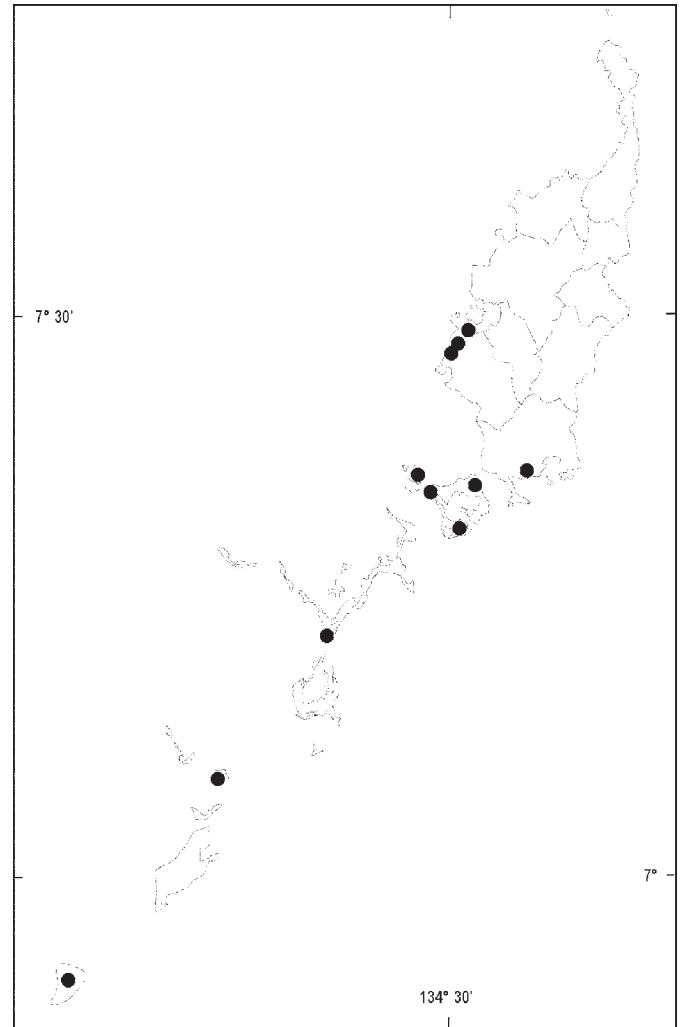

FIGURE 19. Geographic occurrence of *Hemiphyllodactylus ganoklonis* in Palau Islands. Circles indicate specimens represented by museum vouchers. (Image modified from map by D. Dalet.)

G. larutensis, and this should, perhaps be substituted for "Malacca," over 200 miles distant." Following my review of E. Hartert's publications and the locality data from his bird collection, it is evident that Boulenger's assessment is correct and his restriction should be followed.

The type of *Gehyra larutensis* Boulenger and other specimens from Boulenger's descriptions of new frogs and reptiles from the Larut Hills, Perak, are listed as in/ from the Selangor Museum. Presumably, that is their origin, but it appears that Boulenger retained them because the catalog number (1901.3.20.2) of *G. larutensis* indicates that it became part of the British Museum collection in 1901. My identification of the holotype relies on the

BMNH's labeling of the specimen as type, and in most features my measurements and counts match those of Boulenger. My count of the continuous precloacal–femoral pore series, however, is six pores less than Boulenger's count of 42.

I have seen only a single specimen of *H. harterti*, that is, the holotype of *H. larutensis*. In spite of the insufficiency of my observations, I recognize this taxon owing to a unique coloration (from published images) and the values of several mensural and meristic traits lying on the edges of the ranges of those traits for geckos of the Titiwangsa mountain range.

DESCRIPTION.   A bisexual taxon of geckos (Gekkoninae) with robust habitus, slightly compressed trunk and moderately large head (Figures 3, 11, 12), tail round to elliptical in cross section and somewhat shorter than SVL. An adult male (holotype of *H. larutensis*; Figure 12), 35.3 mm SVL, 31 mm TailL, 17.8 mm TrunkL, 8.3 mm HeadL, 6.3 mm HeadW, 3.5 mm SnEye, 2.6 mm NarEye, 2.1 mm EyeD, and 1.8 mm SnW. Proportions: 50% TrunkL/SVL, 24 % HeadL/SVL, 18% HeadW/SVL, 75% HeadW/HeadL, 42% SnEye/HeadL, 31% NarEye/HeadL, 25% EyeD/HeadL, 22% SnW/HeadL, 81% EyeD/NarEye, 29% SnW/HeadW. Scalation: 2 CircNa, 3 SnS, 10 Suplab, 10 Inflab, 9 Chin (anteromedial ones strongly enlarged, ≥2× larger than adjacent ones that are also enlarged), 15 Dorsal, 6 Ventral, 2 CloacS, Subcaud not enlarged, 36 TotPore precloacal and femoral pores continuous with demarcation between two series, digital formulae 3-3-3-3 (forefoot) and 3-3-4-3 (hindfoot). Caecum not pigmented, pigmentation unknown for testis epididymis. Aside from coloration, female morphological traits are detailed in the holotype description below.

Head to trunk dorsally and laterally a yellowish to dusky tan ground color; tail distinctly brighter (lighter) than body and limbs. Light spots in a dorsolateral series from neck to postsacral mark or dark brown dorsolateral stripe from neck merging into dark median border of postsacral mark. Tail uniformly colored.

Major diagnostic features are as follows: bisexual taxon; caecum and (likely) gonadal ducts not pigmented; precloacal–femoral pore series continuous; chin scales bordering mental and first infralabial distinctly enlarged; digital lamellae formulae 3-3-3-3 (forefoot) and 3-3-4-3 (hindfoot); adult SVL < 40 mm; dorsum of head and trunk either nearly uniform tan or with narrow dark dorsolateral stripes and contrasting with lighter tail, outer edge of postsacral mark continuous with caudal color.

Description of holotype: An adult female (Figure 12) , 40.9 mm SVL, 39 mm TailL, 21.5 mm TrunkL, 9.7 mm HeadL, 6.3 mm HeadW, 4.0 mm SnEye, 3.2 mm NarEye, 2.9 mm EyeD, and 2.0 mm SnW. Proportions: 53% TrunkL/SVL, 24% HeadL/SVL, 15% HeadW/SVL, 65% HeadW/HeadL, 41% SnEye/HeadL, 33% NarEye/HeadL, 30% EyeD/HeadL, 21% SnW/HeadL, 91% EyeD/NarEye, 32% SnW/HeadW. Scalation: 3 CircNa, 2 SnS, 10 Suplab, 11 Inflab, 6 Chin (anteromedial ones enlarged, twice as large as adjacent ones that are also enlarged), ? Dorsal, ? Ventral, 1 CloacS, Subcaud not enlarged, 0 PreclPor, 0 TotPore, digital formulae not known. No pigmentation on caecum or oviducts.

Specimen faded to uniform beige dorsally and laterally, somewhat lighter ventrally. Evidence of a dark postsacral mark.

ETYMOLOGY.   Werner (1900) noted that a single specimen (holotype) of this gecko was collected in Malakka by Hartert and deposited in the Berlin collection. Presumably, the Hartert referred to by Werner is Ernest Johann Otto Hartert, an ornithologist who served as the bird curator in L. W. Rothschild's private museum at Tring, UK, between 1892 and 1929. Prior to his employment at Tring, Hartert visited Asia and elsewhere and collected birds, insects, and other animals. He reported his research travels in a popular book, *Aus den Wanderjahren eines Naturforschers* (Hartert, 1901–1902).

DISTRIBUTION.   Presently known from Larut Hills and Gunong Inas, Perak (Figure 20); presumably, it occurs throughout the forest of the Bukit Bintang mountains.

Hemiphyllodactylus insularis Taylor
Philippine slender gecko

Hemiphyllodactylus insularis Taylor, 1918:237 [type locality: "Sumagui, Mindoro" (Philippines); holotype, CM 2052].

DESCRIPTION.   Adults dimorphic, females larger than males: 29.6–37.3 mm (mean ± SD, 33.9 ± 1.82; *n* = 15 females), 28.8–34.4 mm (31.3 mm ± 1.86, *n* = 19 males) SVL; 15.5–19.3 mm (17.8 mm ± 1.08), 14.3–17.7 mm (15.8 mm ± 1.05) TrunkL; 6.6–8.6 mm (7.6 mm ± 0.51), 6.2–8.2 mm (7.2 mm ± 0.51) HeadL; 3.8–5.7 mm (4.8 mm ± 0.48), 4.0–5.8 mm (4.8 mm ± 0.46) HeadW; 2.6–3.7 mm (3.0 mm ± 0.28), 2.1–3.4 mm (2.8 mm ± 0.28) SnEye; 2.0–2.6 mm (2.3 mm ± 0.20), 1.9–2.6 mm (2.2 mm ± 0.17) NarEye; 1.8–2.1 mm (2.0 mm ± 0.11), 1.6–2.1 mm (1.9 mm ± 0.14) EyeD; 1.2–1.4 mm (1.3 mm ± 0.08), 1.0–1.5 mm (1.3 mm ± 0.16) SnW. Adult proportions not dimorphic: 45–58% TrunkL/SVL (mean ± SD, 50.1% ± 2.9), 21–24% HeadL/SVL (22.7%
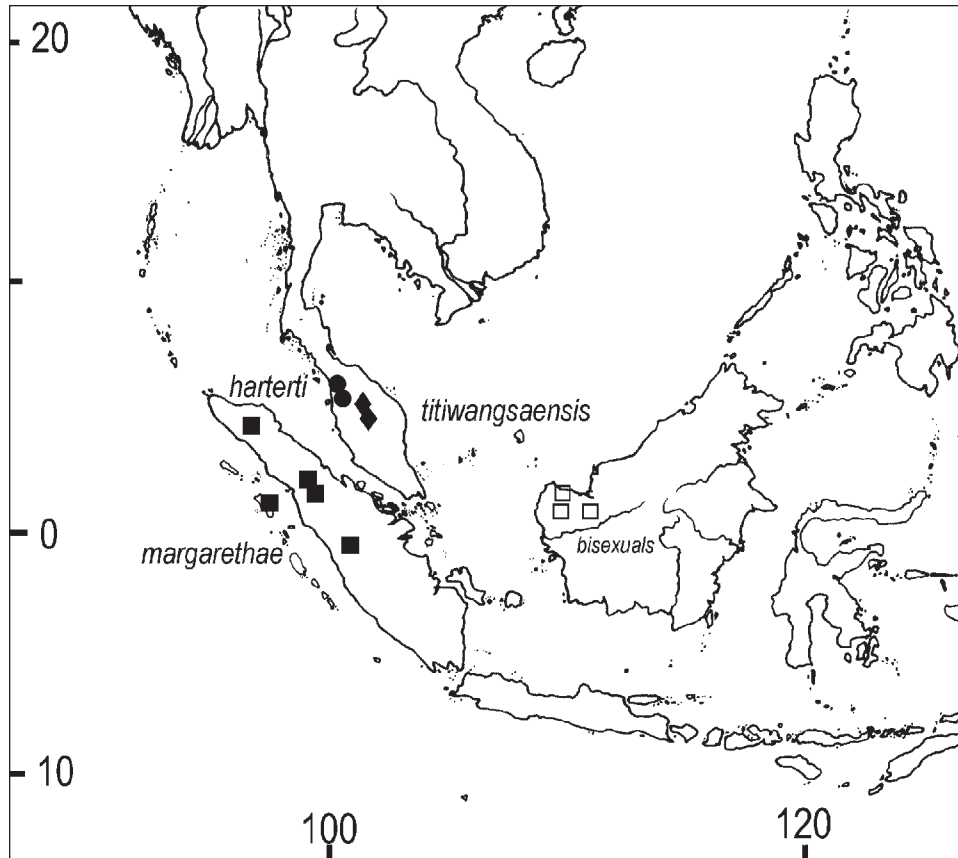
FIGURE 20. Geographic occurrence of *Hemiphyllodactylus harterti*, *H. margarethae*, *H. titiwangsaensis*, and bisexual specimens from Borneo. Symbols: circle, *H. harterti*; diamond, *H. titiwangsaensis*; solid square, *H. margarethae*; open square, bisexuals.

± 0.1), 12–18% HeadW/SVL (14.9% ± 0.1), 54–82% HeadW/HeadL (65.7% ± 5.9), 26–44% SnEye/HeadL (39.4% ± 3.1), 27–42% NarEye/HeadL (31.2% ± 2.5), 23–32% EyeD/HeadL (26.1% ± 1.6), 14–21% SnW/HeadL (17.2% ± 1.8), 74–95% EyeD/NarEye (84.0% ± 5.2), 20–37% SnW/HeadW (26.3% ± 3.2%).

Scalation is predominantly granular from head onto tail, both dorsally and ventrally; ventral trunk scales slightly larger than dorsal ones, 13–18 Dorsal (median ± SD, 16 ± 1.4) and 8–14 Ventral (11 ± 1.6); similarly, subcaudal scales slightly larger than dorsal caudal scales but not plate-like. Cloacal spurs present, modest sized, 0–3 CloacS (1 ± 0.9). Larger scales on lips and snout, rostral largest, rectangular to pentagonal, often slightly concave on dorsomedial edge with slight cleft; 1–4 CircNa (3 ± 0.8), 2–4 SnS (3 ± 0.6); labial scales enlarged from rostral to below eye, becoming progressively smaller in subocular rictus, 9–13 Suplab (10 ± 1.2), 9–11 Inflab (10 ± 0.6); 8–14 Chin (11 ± 1.5), those behind mental slightly or not

enlarged; ear opening distinct with no bordering enlarged scales. Each digit with expanded pad, terminal two phalanges free, arising from within pad on second to fifth digits of fore- and hindfoot and each clawed; pads of these digits each with large triangular apical lamella bordered proximally by lyre-shaped lamellae (scansors); modal digital formulae 3-3-3-3 (forefoot) and 3-4-4-4 (hindfoot) for scansors; first digit of fore- and hindfeet compressed, usually 4 or 5 rectangular lamellae (2–5 fore, 3–6 hind) ventrally, terminal phalanx not free with or without minute claw. Adult females never with precloacal pores, males always with precloacal pores (median ± SD, 9 ± 1.5; range, 6–13) always separated from femoral pore series, 17–38 TotPore (27 ± 5.35).

In alcohol, light to medium brown ground color dorsally and laterally from head to tail; top of head with scattering of small dark brown blotches, lateral dark brown stripe from loreal to shoulder variously developed (barely visible to sharply defined); dorsally on trunk, dark blotches

variously arranged from series of parasagittal elongate spots through randomly arranged spots creating irregular narrow transverse bars to nearly absent; dark lateral stripe on trunk typically series of lateral dark spots or blotches; dorsolateral series of light spots from temporal area to inguina, posteriormost one enlarged and forming anterior end of lateral light arm of postsacral mark; well-defined postsacral mark in all individuals with large pentagonal middorsal dark brown mark bordered behind and on sides by light (whitish) base and arms, which are edged laterally and caudally in dark brown. Tail usually lighter brown than trunk with amorphous dark smudges middorsally. Venter, chin to tail, dusky cream owing to dark spot in most ventral scales.

In life, light dusky tan to reddish brown ground color dorsally and laterally from head to hips; pattern of markings as described for preserved individuals. Light dorsolateral spots and light area of postsacral mark brick red.

Major diagnostic features are as follows: bisexual taxon; pigmented caecum and oviducts; no precloacal–femoral pores in females, present in males, precloacal and femoral pore series separated; chin scales bordering mental and first infralabial not greatly enlarged; digital lamellae

formulae 3-3-3-3 (forefoot) and 3-4-4-4 (hindfoot); average adult SVL ~34, 31 mm (females, males); series of red spots dorsolaterally on trunk and bright postsacral bar of red and dark brown.

Description of holotype: An adult male (Figure 21), 30.2 mm SVL, 14.7 mm TrunkL, 6.9 mm HeadL, 2.6 mm HeadW, 4.0 mm SnEye, 1.9 mm NarEye, 1.8 mm EyeD, and 1.2 mm SnW. Proportions: 49% TrunkL/SVL, 23% HeadL/SVL, 13% HeadW/SVL, 58% HeadW/HeadL, 38% SnEye/HeadL, 28% NarEye/HeadL, 26% EyeD/HeadL, 17% SnW/HeadL, 95% EyeD/NarEye, 30% SnW/HeadW. Scalation: 3 CircNa, 3 SnS, 10 Suplab, 11 Inflab, 11 Chin (anteromedial ones only slightly larger than adjacent ones), 15 Dorsal, 11 Ventral, 3 CloacS, Subcaud not enlarged, 9 PreclPor, 27 TotPore precloacal and femoral series separated, digital formulae 3-3-3-3 (forefoot) and 3-4-4-4 (hindfoot). Pigmented caecum, pigmentation unknown for testis epididymis.

Faded, body ground color brown.

ETYMOLOGY. Taylor (1918) did not explain his choice of the epithet *insularis*, presumably because he assumed the name was self-explanatory; *insularis* is a Latin adjective for of islands.

FIGURE 21. Holotype of *Hemiphyllodactylus insularis* Taylor, 1918 (CM 2052): (A) dorsal view of whole body, (B) ventral view of head, and (C) ventral view of posterior half of trunk. (Photographs by M. McNaugher.)

VARIATION. The means or medians and ranges are detailed in the preceding Description section. Males are smaller, statistically significantly so, than females, but the difference in average size is slight (~2.5 mm). None of the meristic traits shows significant dimorphism among adults, other than presence of precloacal and femoral pores in males and their absence in females. Variation of most scalation traits is modest to low with the values of most traits equaling the median. Chin scales are usually small, although a few individuals have a modest enlargement of those touching the mental and first supralabial. There are six digital formulae each for forefoot and hindfoot. Forefoot formulae range from 3-3-3-3 (66%) to 3-4-4-4 with only 3-3-4-3 (17%) also occurring in more than two individuals. Hindfoot formulae range from 3-3-4-3 to 4-5-5-4; 3-4-4-4 is the most frequent (49%), followed by 3-4-4-3 (17%) and 4-4-5-4 (14%).

DISTRIBUTION. *Hemiphyllodactylus insularis* occurs throughout the Philippine Islands (Figure 22) from Mindoro to Mindanao and westward on both the Palawan and Sulu Archipelago arcs. The presence on both these latter island groups recommends a reexamination of the bisexual Bornean *Hemiphyllodactylus*.

Hemiphyllodactylus margarethae Brongersma
Sumatran slender gecko

Hemiphyllodactylus margarethae Brongersma, 1931:11 [type locality: "Fort de Kock, Sumatra" (Bukittinggi, Sumatera Barat); holotype, ZMA 11095].

COMMENT. Brongersma (1932:218 [footnote]) noted that while the *H. margarethae* description was in press and after he had examined additional *Hemiphyllodactylus* specimens, he attempted to suppress the new name in page proofs, but his recommended changes were not made.

DESCRIPTION. A bisexual taxon of geckos (Gekkoninae) with robust habitus, slightly compressed trunk and moderately large head (see Figures 3, 23), tail round in cross section and subequal to SVL. Adults not dimorphic: 36.0–46.9 mm SVL (mean ± SD, 40.8 mm ± 3.6], n = 8), 14.5–25.4 mm TrunkL (20.6 mm ± 3.3), 8.2–10.4 mm HeadL (9.6 mm ± 0.87), 5.8–8.2 mm HeadW (6.8 mm ± 0.86), 3.3–4.7 mm SnEye (4.1 mm ± 0.56), 2.7–3.6 mm NarEye (3.2 mm ± 0.40), 1.6–2.5 mm EyeD (2.1 mm ± 0.35), 1.4–1.9 mm SnW (1.7 mm ± 0.23). Adult proportions: 40–54% TrunkL/SVL (mean ± SD, 50.3% ± 4.8), 21–26% HeadL/SVL (23.5% ± 1.6), 15–19% HeadW/SVL (16.7% ± 1.3), 66–79% HeadW/HeadL (71.2% ±
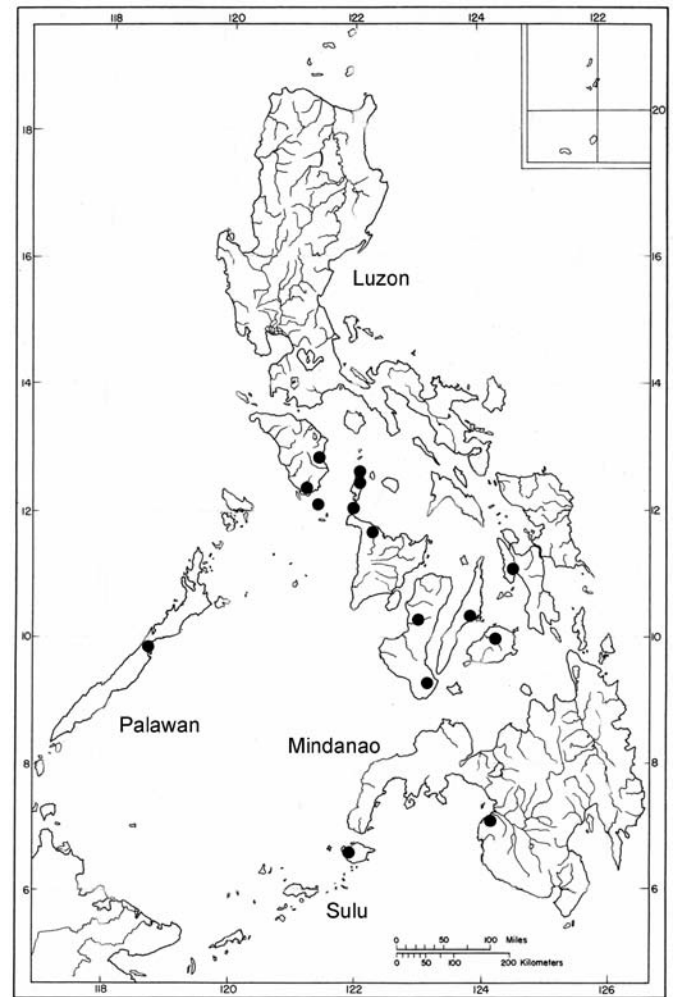

FIGURE 22. Geographic occurrence of *Hemiphyllodactylus insularis* in the Philippine Islands. Not all localities in the same area are plotted. Circles indicate specimens represented by museum vouchers and whose specific identity is confirmed.

4.4), 39–46% SnEye/HeadL (42.6% ± 2.4), 29–35% NarEye/HeadL (33.0% ± 2.0), 16–25% EyeD/HeadL (22.0% ± 3.6), 15–19% SnW/HeadL (17.3% ± 1.4), 47–81% EyeD/NarEye (67.0% ± 12.6), 22–28% SnW/HeadW (24.3% ± 1.9%).

Scalation is predominantly granular from head onto tail, both dorsally and ventrally; ventral trunk scales slightly larger than dorsal ones, 11–17 Dorsal (median ± SD, 12.5 ± 2.3) and 6–12 Ventral (7.5 ± 2.3); similarly, subcaudal scales slightly larger than dorsal caudal scales but not plate-like. Cloacal spurs present, modest sized, 1–2 CloacS (2 ± 0.5). Larger scales on lips and snout, rostral largest, rectangular to pentagonal, often slightly concave on dorsomedial

edge with slight cleft; 2–3 CircNa (3 ± 0.4), 2–4 SnS (3 ± 0.6); labial scales enlarged from rostral to below eye, becoming progressively smaller in subocular rictus, 10–13 Suplab (11 ± 1.2), 9–12 Inflab (10 ± 0.9); 6–11 Chin (7.5 ± 2.0), those behind mental distinctly enlarged; ear opening distinct with no bordering enlarged scales. Each digit with expanded pad, terminal two phalanges free, arising from within pad on second to fifth digits of fore- and hindfoot and each clawed; pads of these digits each with large triangular apical lamella bordered proximally by lyre-shaped lamellae (scansors); modal digital formulae likely 4-4-4-4 (forefoot) and 4-5-5-5 (hindfoot) for scansors; first digit of fore- and hindfeet compressed, usually 5 rectangular lamellae (4–8 fore, 4–7 hind) ventrally, terminal phalanx not free with or without minute claw. Adult females often with precloacal pores series (0–12 PreclPor), males (only one adult in sample) always with precloacal pores (median 11) always separated from femoral pore series, 0–29 (female) 26 (male) TotPore.

Coloration, no images of living specimens and preserved specimens pattern indistinct owing to fading.

Major diagnostic features are as follows: bisexual taxon; unpigmented caecum, oviducts pigmented or not; if present, femoral pore series separate from precloacal pore series; chin scales bordering mental and first infralabial distinctly enlarged; digital lamellae formulae 4-4-4-4 (forefoot) and 4-5-5-5 (hindfoot); average adult SVL ~41 mm.

Description of holotype: An adult male (Figure 23), 38.8 mm SVL, 40 TailL, 18.7 mm TrunkL, 9.9 mm HeadL, 7.5 mm HeadW, 4.3 mm SnEye, 3.4 mm NarEye, 1.6 mm EyeD, and 1.9 mm SnW. Proportions: 48% TrunkL/SVL, 25% HeadL/SVL, 19% HeadW/SVL, 76% HeadW/HeadL, 43% SnEye/HeadL, 34% NarEye/HeadL, 16% EyeD/HeadL, 19% SnW/HeadL, 47% EyeD/NarEye, 25% SnW/HeadW. Scalation: 3 CircNa, 3 SnS, 10 Suplab, 11 Inflab, 6 Chin (anteromedial ones distinctly enlarged, see Figure 7C), 13 Dorsal, 7 Ventral, 2 CloacS, Subcaud not enlarged, 11 PreclPor, 26 TotPore, separate precloacal and femoral series, digital formulae 4-5-5-5 (forefoot) and 5-5-6-5 (hindfoot). Caecum and testis epididymis presumably unpigmented.

Body ground color faded to pinkish beige, small paired dark blotches dorsally on trunk; paratype (ZMA 11096) has a hint of a postsacral mark.

Etymology. The origin of the epithet *margarethae* is unknown.

Variation. The means or medians and ranges are detailed in the preceding Description section. Sample is small and specimens old and generally poorly preserved; hence comments on variation are inappropriate.

FIGURE 23. Types of *Hemiphyllodactylus margarethae* Brongersma, 1931: left, ZMA 11095 holotype, male; right, 11096 paratype, female. (Photograph by G. Zug.)

Distribution. With a single exception, the *H. margarethae* specimens derive from the central mountain ranges of central and northern Sumatra (Figure 20), extending from Bukittinggi in the south to Takengon in the north. The Nias island locality is the exception and requires confirmation.

Hemiphyllodactylus titiwangsaensis Zug, new species
Titiwangsan slender gecko

Holotype. ZRC 2.4782, adult male from Malaysia, Pahang Province, Cameron Highlands, Gunong Brinchang (= Berincang) summit area, collected by H. H. Tan and others, 25 June 2000.

Paratypes. All subsequent specimens are from Malaysia, Pahang Province; that datum is removed from each subsequent locality for brevity. ZFMK 32284–286, Cameron Highlands, Tana Ratah (=Tanah Rata), collected by Dietmar Kiehlmann, July 1980; ZRC 2.4780–781, 2.4783–785, collecting data same as holotype; ZRC 2.4832, Cameron Highlands, Tanah Rata, Bala's Lodge, collected by H. H. Tan, 4 May 2000; ZRC 2.5165, Cameron Highlands, Parit Falls, T. M. Leong, and L. J. Lim, 30 July 2001; ZRC 2.5419, Cameron Highlands, Parit Falls, collected by B. L. Lim and K. K. P. Lim, 10 May 2002;

ZRC 2.5942, Cameron Highlands, Telom Valley, Kuala Terla 4000–4500′, collector unknown, March 1935; ZRC 2.5943, Cameron Highlands, Telom Valley, Gunong Siku at ~4500′, collector unknown, March 1935. Adult females: ZFMK 32284, 32286; ZRC 2.4780–4781, 2.4785, 2.4832, 2.5165, 2.5943; adult males: ZFMK 32385; ZRC 2.4783–4784, 2.5419, 2.5942.

DESCRIPTION.   Bisexual taxon of geckos (Gekkoninae) with robust habitus, slightly compressed trunk and moderately large head (see Figures 3, 11, 24), tail round to elliptical in cross section and somewhat shorter than SVL. Adults not dimorphic: 36.5–62.1 mm (mean ± SD, 49.2 mm ± 6.34; n = 15) SVL; 18.1–32.5 mm (23.3 mm ± 3.69) TrunkL; 8.9–13.8 mm (12.0 mm ± 1.18) HeadL; 6.1–10.2 mm (8.2 mm ± 0.98) HeadW; 3.4–5.8 mm (4.9 mm ± 0.60) SnEye; 2.6–4.4 mm (3.6 mm ± 0.42) NarEye; 2.4–3.6 mm (3.0 mm ± 0.31) EyeD; 1.4–2.6 mm (2.0 mm ± 0.32) SnW. Adult proportions: 42–50% TrunkL/SVL (mean ± SD, 46.4% ± 3.4), 23–27% HeadL/SVL (24.6% ± 1.4), 16–19% HeadW/SVL (16.9% ± 1.0), 64–73% HeadW/HeadL (68.5% ± 3.5), 37–43% SnEye/HeadL (40.7% ± 2.1), 26–32% NarEye/HeadL (29.4% ± 2.1), 21–30% EyeD/HeadL (25.6% ± 2.5), 14–21% SnW/HeadL (16.5% ± 2.5), 68–94% EyeD/NarEye (85.4% ± 9.6), 21–31% SnW/HeadW (23.8% ± 3.2%).

Scalation is predominantly granular from head onto tail, both dorsally and ventrally; ventral trunk scales slightly larger than dorsal caudal scales, 14–19 Dorsal (median ± SD, 16 ± 1.9) and 7–9 Ventral (7 ± 1.0); similarly, subcaudal scales slightly larger than dorsal ones but not plate-like. Cloacal spurs present, modest sized, 1–4 CloacS (3 ± 1.0). Larger scales on lips and snout, rostral largest, rectangular to pentagonal, often slightly concave on dorsomedial edge with slight cleft; 3 CircNa (3 ± 0.0), 1–3 SnS (3 ± 0.8); labial scales enlarged from rostral to below eye, becoming progressively smaller in subocular rictus, 9–11 Suplab (10 ± 0.7), 8–10 Inflab (9 ± 0.7); 8–9 Chin (9 ± 0.5), those behind mental distinctly enlarged; ear opening distinct with no bordering enlarged scales. Each digit with expanded pad, terminal two phalanges free, arising from within pad on second to fifth digits of fore- and hindfoot and each clawed; pads of these digits each with large triangular apical lamella bordered proximally by lyre-shaped lamellae (scansors); modal digital formulae 3-4-4-4 (forefoot) and 4-5-5-5 (hindfoot) for scansors; first digit of fore- and hindfeet compressed, usually 5 or 7 rectangular lamellae (4–6 fore, 5–8 hind) ventrally, terminal phalanx not free with or without minute claw. Adult females never with precloacal pores; males always with continuous precloacal–femoral pore series 17–39 TotPore (median ± SD, 21 ± 7.95).

In life, dorsal and lateral ground color ranges from light grayish tan to medium brown, head to tail occasionally distinctly lighter than neck and trunk (Figure 11). This lightness is emphasized by absence or diffuseness of dark markings on head. Neck and trunk bear numerous transverse dark brown irregularly shaped bars, lighter interspaces typically narrower than dark bars. Bars extend onto sides; dorsolaterally in shoulder area bars are darker, creating an impression of dark dorsolateral stripe. Dark lateral stripe from loreal to neck, occasionally to midneck. Dark stripe bordered above by cream to beige stripe from canthus rostralis to shoulder, often continuing as series of spots or dashes on trunk and at inguina becoming narrow arm of postsacral mark; center dark spot of mark absent to small. Tail usually lighter than trunk and distinctly banded in light and dark, relative size of which very variable. (Coloration from images by H. Ota and Chan-ard et al., 1999.)

Coloration in alcohol is muted, although dark and light pattern usually persists. Ventrally from chin onto tail, uniform light cream in most individuals, brown in a few. Females seem to be more boldly patterned than males.

Major diagnostic features are as follows: bisexual taxon; caecum and gonadal ducts not pigmented; precloacal–femoral pore series continuous in males (TotPore 17–39), absent in females; chin scales bordering mental and first infralabial distinctly enlarged; digital lamellae formulae usually 3-4-4-4 (forefoot) and 4-4-5-5 or 4-5-5-5 (hindfoot); average adult SVL ~49 mm; dorsal and lateral trunk pattern of dark brown irregular transverse bands, muted postsacral bar of narrow white arms onto hips.

Description of holotype: An adult male (Figure 24), 56.9 mm SVL, 48 mm TailL (regenerated), 24.1 mm TrunkL, 13.2 mm HeadL, 9.6 mm HeadW, 5.4 mm SnEye, 3.9 mm NarEye, 3.0 mm EyeD, and 2.4 mm SnW. Proportions: 42% TrunkL/SVL, 23% HeadL/SVL, 17% HeadW/SVL, 73% HeadW/HeadL, 41% SnEye/HeadL, 28% NarEye/HeadL, 23% EyeD/HeadL, 18% SnW/HeadL, 81% EyeD/NarEye, 25% SnW/HeadW. Scalation: 3 CircNa, 3 SnS, 10 Suplab, 9 Inflab, 8 Chin (anteromedial ones enlarged), 16 Dorsal, 7 Ventral, 3 CloacS, Subcaud not enlarged, precloacal and pore series continuous, 30 TotPore, digital formulae 4-4-5-4 (forefoot) and 4-5-5-5 (hindfoot). No pigmentation on caecum or oviducts.

Specimen brown dorsally and laterally with scattered indistinct dark brown markings, somewhat lighter ventrally. Postsacral mark indistinct, small median dark spot on first tail segment, anterior arms muted. In life, the ventral surface of the tails (type series) were orangish pink.

ETYMOLOGY.   These geckos occur in the south central region of the Banjaran Titiwangsa; hence the

FIGURE 24. Types of *Hemiphyllodactylus titiwangsaensis*: left to right, ZRC 2.4780–2.4785; 2.4782 is the holotype. (Photograph by G. Zug.)

taxon is a resident (likely endemic) of Titiwangsa and so named.

VARIATION. The means or medians and ranges are detailed in the preceding Description section. Adults are not dimorphic, and both sexes have broad ranges of adult sizes, females 42.2–62.1 mm SVL and males 36.5–56.9 mm. This broad range yields a modest increase in variation among the mensural traits (CV = 8–17%). Larger (≥46 mm SVL) adults are distinctly robust-bodied geckos.

Scalation has low variation with the exception of phalangeal formulae. Seven forefoot formulae range from 2-3-3-3 to 4-5-5-5; however, 3-4-4-4 is the mode and median with a uniform and sharp drop in number of individuals on each side of the mode. Hindfoot formulae (8) are dominated by 4-4-5-5 (*n* = 3) and 4-5-5-5 (7); the other six formulae observed have low (*n* = 1 each) representation; 3-3-3-3 is the lowest.

Coloration has two patterns. The transverse bar pattern (somewhat *Lepidodactylus lugubris*-like) described above occurs in the majority of individuals, and a few individuals show gradation from this pattern into a ragged spotted one.

DISTRIBUTION. All specimens derive from localities within Banjaran Titiwangsa (Figure 20) and particularly from Fraser Hill and Cameron Highland areas. At both sites, *H. titiwangsaensis* occurs in forest and on and around buildings. I assume that these geckos occur more broadly in moist evergreen forest of the Titiwangsa mountain range and that the present vouchers represent the most accessible areas.

Hemiphyllodactylus yunnanensis (Boulenger) Asian slender gecko

Gehyra yunnanensis Boulenger, 1903:429 [type locality: "Yunnan Fu" (= Kumning, Yunnan Province, China); lectotype, BMNH 1904.1.26.1].

Hemiphyllodactylus typus chapaensis Bourret, 1937:60 [type locality: "Chapa" (Sa Pá [also Lao Cai], Vietnam); holotype, MNHN 1948.43].

Hemiphyllodactylus yunnanensis longlingensis Zhou and Yang in Zhou et al., 1981:203 [type locality: Longling Junior High School in Longling County, Yunnan Province (alt. 1530 m) (China) (original in Chinese)].

Hemiphyllodactylus yunnanensis jinpingensis Zhou and Yang in Zhou et al., 1981:204 [type locality: Jinpling Junior High School in Jinping County, Yunnan Province (alt. 1260 m) (China) (original in Chinese)].

Hemiphyllodactylus yunnanensis dushanensis Zhou and Yang in Zhou et al., 1981:206 [type locality: Dushan Junior High School in Dushan County, Guizhou Province (alt. 970 m) (China) (original in Chinese)].

COMMENTS. Readers are reminded that *H. yunnanensis* is considered here to include the highland populations of *Hemiphyllodactylus* across southern China and adjacent northern Southeast Asia from Myanmar to Vietnam. The taxonomic status of the "lowland" populations of Southeast Asia and Hong Kong remains unresolved owing to the sparsity of vouchers in numbers and geography.

Boulenger (1903) identified two syntypes "male and young." Both specimens (BMNH 1904.1.26.1–2; Figure 25) are extant. I designate the adult male (BMNH 1904.1.26.1) as the lectotype of *Gehyra yunnanensis* Boulenger.

Bourret said in the type description: "J'ai pris à Chapa une femelle à queue reconstituée (S130) . . ." Brygoo (1990:44) and I interpret this statement as a description based on a single female specimen. This interpretation conflicts with Guibe's (1954) type catalog listing of two specimens; the sex of neither is identified by Guibe, although

FIGURE 25. Lectotype of *Gehyra yunnanensis* Boulenger, 1903 (BMNH 1904.1.26.1): (A) dorsal view of whole body, (B) ventral view of throat and chin, and (C) ventral view of pelvic area. (Photographs by G. Zug.)

one is noted to be damaged and 56 mm long. Brygoo noted that of the two specimens labeled syntypes, both possess Bourret's registration numbers and one (S130) is unambiguously the holotype of *H. typus chapaensis* Bourret. Also, the holotype is 43 mm SVL (Brygoo 1990:44) and 42.7 mm (my measurement), and 33 mm (Bourret, 1937:60). This disparity, yet similarity, suggests that Bourret accidentally entered 33 instead of 43.

DESCRIPTION. A bisexual taxon of geckos (Gekkoninae) with robust habitus, slightly compressed trunk and moderately large head (Figures 3, 11, 25), tail round in cross section and typically shorter than SVL. Adults dimorphic, females larger than males: 31.9–49.3 mm (mean ± SD, 40.7 mm ± 4.44; *n* = 33), 25.5–46.4 mm (37.9 mm ± 4.58, *n* = 28) SVL; 15.4–26.5 mm (19.5 mm ± 2.93), 12.8–22.5 mm (17.9 mm ± 2.30) TrunkL; 7.6–11.5 mm (9.5 mm ± 0.98), 6.7–10.3 mm (8.8 mm ± 0.89) HeadL; 5.4–8.4 mm, (6.8 mm ± 0.95), 4.8–7.4 mm (6.3 mm ± 0.76) HeadW; 3.0–5.2 mm (3.9 mm ± 0.55), 2.4–4.7 mm (3.7 mm ± 0.50) SnEye; 2.1–4.0 mm (3.0 mm ± 0.44), 1.9–3.4 mm (2.8 mm ± 0.37) NarEye; 1.9–3.2 mm (2.4 mm ± 0.31), 1.6–3.0 mm (2.2 mm ± 0.27) EyeD; 1.0–2.2 mm (1.7 mm ± 0.25), 0.9–2.0 mm (1.5 mm ± 0.25) SnW. Adult proportions not dimorphic: 40–55% TrunkL/SVL (mean ± SD, 47.4% ± 3.1), 21–26% HeadL/SVL (23.3% ± 1.0), 14–22% HeadW/SVL (16.7% ± 1.8), 59–83% HeadW/HeadL (71.9% ± 6.5), 34–46% SnEye/HeadL (41.4% ± 2.5), 26–35% NarEye/HeadL (31.4% ± 2.1), 22–29% EyeD/HeadL (25.1% ± 1.7), 11–22% SnW/HeadL (17.3% ± 2.0), 63–100% EyeD/NarEye (80.3% ± 6.8), 15–36% SnW/HeadW (24.3 ± 3.6%).

Scalation is predominantly granular from head onto tail, both dorsally and ventrally; ventral trunk scales slightly larger than dorsal ones, 9–18 Dorsal (median ± SD, 13 ± 1.8) and 6–12 Ventral (8 ± 1.1); similarly, subcaudal scales slightly larger than dorsal caudal scales but not plate-like. Cloacal spurs usually present, modest sized, 0–2 CloacS (1 ± 0.3). Larger scales on lips and snout, rostral largest, rectangular to pentagonal, often slightly concave on dorsomedial edge with slight cleft; 2–4 CircNa (3 ± 0.2), 2–5 SnS (3 ± 0.7); labial scales enlarged from rostral to below eye, becoming progressively smaller in subocular rictus, 8–13 Suplab (10 ± 1.0), 8–12 Inflab (10 ± 1.1); 6–11 Chin (8 ± 1.1), those behind mental moderately to distinctly enlarged; ear opening distinct with no bordering enlarged scales. Each digit with expanded pad, terminal two phalanges free, arising from within pad on second to fifth digits of fore- and hindfoot and each clawed; pads of these digits each with large triangular apical lamella bordered proximally by
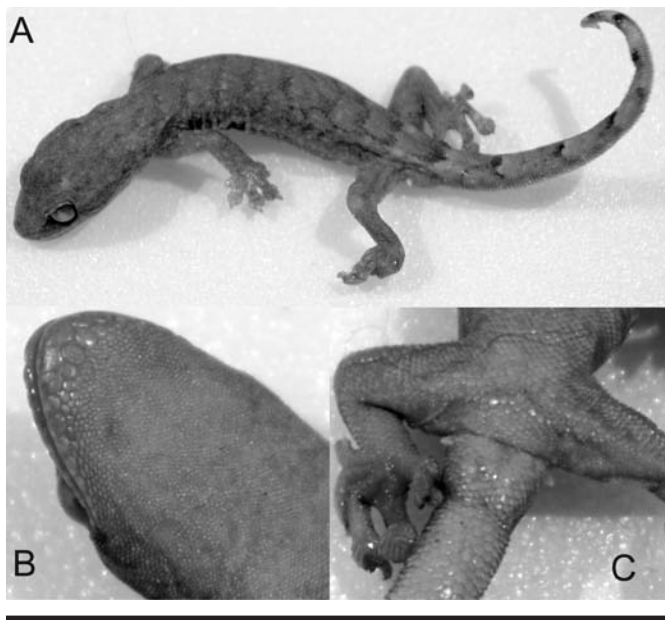
lyre-shaped lamellae (scansors); modal digital formulae 3-3-3-3 (forefoot) and 3-4-4-4 (hindfoot) for scansors; first digit of fore- and hindfeet compressed, usually 4 and 5 rectangular lamellae (4–6 fore, 4–7 hind) ventrally, terminal phalanx not free with or without minute claw. Adult females rarely with precloacal–femoral pore series (7–9 PreclPor, *n* = 2; 0–19 TotPore), males always with continuous precloacal–femoral pore series 11–25 TotPore (median ± SD, 20.0 ± 3.26).

In life, light grayish brown to medium reddish brown ground color dorsally and laterally from head to tail base; top of head with scattering of small dark brown marks, lateral dark brown stripe from loreal to shoulder bordered above by white to tan stripe to end of head; dorsally on trunk, narrow dark brown transverse lines to squiggles, dorsolateral medium-sized light spots from neck to above hindlimb and laterally dark lateral stripe occasionally across neck to anterior trunk and thereafter fragmented to dark dashes or diffuse brown marks; typically, area between dorsolateral light spots and dark lateral stripe lighter than dorsal ground color; postsacral mark small to large blotch bordered behind by rectangular white spot, no anterior extensions; tail ground color lighter than trunk with series of transverse blotches of narrow dark brown bordered behind by broader area of light tan. Venter dusky, tail base pinkish to light orange blush.

In alcohol, pattern as above and fading toward a uniform light to medium brown with brown marks.

Major diagnostic features are as follows: bisexual taxon; caecum and gonadal ducts not pigmented; precloacal–femoral pore series continuous in males (TotPore 11–25), usually absent in females; chin scales bordering mental and first infralabial distinctly enlarged; digital lamellae formulae usually 3-3-3-3 (forefoot) and 3-4-4-4 (hindfoot); average adult female SVL ~41 mm, males ~39 mm; dorsal trunk pattern of narrow dark brown irregular transverse bands bordered dorsolaterally by longitudinal series of light spots, postsacral bar of dark and light with no anterior extensions dorsolaterally.

Description of lectotype: An adult male, 40.3 mm SVL, ~41 regenerated TailL, 20.1 mm TrunkL, 9.9 mm HeadL, 7.8 mm HeadW, ~4.3 mm SnEye, ~3.3 mm NarEye, ~2.6 mm EyeD, and ~1.8 mm SnW. Proportions: 50% TrunkL/SVL, 25% HeadL/SVL, 19% HeadW/SVL, 79% HeadW/HeadL, ~44% SnEye/HeadL, ~34% NarEye/HeadL, ~26% EyeD/HeadL, ~18% SnW/HeadL, ~79% EyeD/NarEye, ~26% SnW/HeadW. Scalation: 3 CircNa, 3+ SnS, 9 Suplab, 9 Inflab, ±10 Chin (anteromedial ones distinctly larger than adjacent ones), ~16 Dorsal, ~8 Ventral, 2 CloacS, Subcaud not enlarged, precloacal and femoral pore series continuous 36 TotPore, digital formulae (estimate) 3-3-3-3 (forefoot) and 3-4-4-4 (hindfoot). Pigmentation of caecum and testis epididymis unknown, likely no pigmentation.

Body ground color grayish brown above and below, scattered dark spots and small dark spots middorsally, no lateral spotting on trunk; dark dorsolateral stripe from eye to shoulder, lateral stripe from in front of eye to end of head.

Caecum not visible through body wall; not dissected so unable to confirm gonadal pigmentation.

ETYMOLOGY.   The name *yunnanensis* identifies this species as the gecko from Yunnan, the type locality of Boulenger's new species.

VARIATION.   The means or medians and ranges are detailed in the preceding Description section. Adults are dimorphic in size, and both sexes have broad ranges of adult sizes. The variation in mensural and meristic traits is examined in the bisexual portion of the Character Analysis section.

DISTRIBUTION.   Highlands of southwestern China and adjacent uplands from the western edge of the Shan Plateau in Myanmar, across northern Thailand, Laos, and Vietnam (Figure 16). The southern limits of the distribution are ill-defined owing to limited sampling of these geckos through much of Asia.

KEY TO THE SPECIES OF *HEMIPHYLLODACTYLUS*

1. Chin scales bordering mental scale posteriorly distinctly enlarged [Figure 7C,D] appear as a pair of scales labeled postmentals in other geckos; caecum and gonadal peritoneum white [Figure 2C] 5

1′. Chin scales bordering mental scale posteriorly slightly or not enlarged [Figure 7A,B], their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black [Figure 2B] 2

2. Adult females with actively secreting precloacal and femoral pores; unisexual species, all individuals are females; adult size often >36 mm SVL . . . . *H. typus*

2′. Adult females with no or fewer than five secreting precloacal pores; populations of females and males; adult size seldom >38 mm SVL 3

3. Usually two U-shaped digital lamellae under fourth digit of forefoot; dorsal trunk pattern bold, transverse dark blotches, longitudinal series of white dorsolateral spots and postsacral mark of dark brown and orange [Figure 11A] . . . . ***H. aurantiacus***

3′. Three or four U-shaped digital lamellae under fourth digit of forefoot; dorsal trunk pattern muted, faded and small dark blotches or widely separated dark spots [Figure 11F]; postsacral mark with U- or V-shaped outer edge of yellow or red; dorsolateral spots yellow or red 4

4. Total number precloacal and femoral pores (TotPore) usually <24 (16–28) in males; forefoot digital lamellar formula usually 3-4-4-3; postsacral mark outer edge yellow to pinkish yellow . . . . ***H. ganoklonis***

4′. Total number precloacal and femoral pores (TotPore) usually >24 (17–38) in males; forefoot digital lamellar formula usually 3-3-3-3; postsacral mark outer edge red . . . . ***H. insularis***

5. Precloacal and femoral pore series separate; females commonly with precloacal pores; forefoot digital lamellar formula usually 4-4-4-4 . . . . ***H. margarethae***

5′. Precloacal and femoral pore series continuous; females usually lack precloacal pores.: forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4 6

6. Adults large, usually >45 mm SVL; precloacal–femoral pore series usually >22 (17–39) pores; hindfoot digital lamellar formula usually 4-4-5-5 or 4-5-5-5; postsacral mark with anterior arms . . . . ***H. titiwangsaensis***

6′. Adults moderate size, usually <42 mm SVL; hindfoot digital lamellar formula usually 3-3-3-3 or 3-4-4-4, occasionally higher; postsacral mark without anterior arms 7

7. Trunk usually with distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with >30 pores . . . . ***H. harterti***

7′. Trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous with <26 pores 8

8. Precloacal and femoral pore series usually >18 pores; hindfoot digital lamellar formula usually 3-4-4-4; postsacral mark of anterior dark blotch and posterior larger light bar . . . . ***H. yunnanensis***

8′. Precloacal and femoral pore series usually <18 pores; hindfoot digital lamellar formula usually 4-5-5-4; postsacral mark absent or muted dark transverse bar . . . . Hong Kong population

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Appendix 1: Character Definitions

Many of the characters examined and recorded in this study are used broadly in other systematics studies of geckos. I use the abbreviations proposed by me previously (Zug, 1998) for conciseness and for permitting quick identification of the characters. Most characters are defined in Zug et al. (2003). Any not defined there or that are defined differently for *Hemiphyllodactylus* are presented in Table A1.1 below. All measurements were recorded in millimeters to the nearest 0.1 mm and from the right side; bilateral meristic characters were also recorded from right side.

TABLE A1.1. Abbreviations and definitions for characters examined.

Character class and abbreviation	Character name	Definition
Mensural characters		
EyeD	Orbit diameter	Maximum horizontal diameter of exposed eyeball
HeadL	Head length	
HeadW	Head width	
NarEye	Nares–eye length	
SnEye	Snout–eye length	
SnW	Snout (internarial) width	
SVL	Snout–vent length	
TailL	Tail length	
TrunkL	Trunk length	
Meristic characters of scalation		
Chin	Chin scales	Number of scales touching internal edge of infralabials and mental from juncture of 2nd and 3rd infralabials on left and right
CircNa	Circumnasal scales	
CloacS	Cloacal spurs	
Dorsal	Dorsal scales	Number of scales longitudinally at midbody on dorsum contained within one EyeD
Inflab		As for Suplab
PoreC	Femoral and precloacal pores series	FemPor and PreclPor series continuous or separated
PreclPor		
SnS	Scales between supranasals	Number of scales touching rostral scale between left and right supranasals
Subcaud		Scales subequal to dorsal scales or enlarged into plates
Suplab	Supralabial scales	Number of enlarged scales from rostral to top of mouth curve, usually equivalent to end of orbit
TotPore	Total number of secreting pores	Total number of left and right femoral pores and PreclPor
Ventral	Ventral scales	Number of scales longitudinally at midbody on venter contained within one EyeD
1FingLm	First digit lamellae	Number of lamellae (wider than long) on 1st digit of forefoot
1ToeLm	First digit lamellae	Number of lamellae (wider than long) on 1st digit of hindfoot
2-5FingLm, 2-5ToeLm	Second to fifth digit lamellae	Number of entire, U-shaped subdigital lamellae (=scansors) on enlarged pad of 2nd to 5th digit, single apical lamella not counted, only large U-shaped lamellae touching edge of pad
Meristic characters of coloration		
CaecMel	Pigmentation of caecum	Caecum pigmented or not
OrbStrp	Postorbital stripe	Dark lateral stripe from eye to mid-neck or beyond, absent or present
OvidMel	Pigmentation of oviduct	Oviduct pigmented or not
PostocS	Postocular spots	Number of light spots above OrbStrp from behind eye to front of shoulder

Appendix 2: Specimens Examined

LOCALITY SAMPLES

The specimens are segregated by the geographic-specific samples. These samples are arranged from east to west and, for those within similar longitudinal bands, from north to south. The number of specimens listed below for a locality can exceed the number of individuals in a locality sample [SMALL CAP NAME IN BRACKETS] because data were not collected on all specimens due to size or state or preservation, although the specimen's specific identity was confirmed. Catalog numbers for primary type specimens are in **bold**.

Hemiphyllodactylus typus

HAWAIIAN ISLANDS [HAWAI]. No island given: AMNH 22340, MCZ R20268, R154043, USNM 21220. Hawaii: USNM 23459–460, 310815–816, 518722, 570745–748. Kauai: USNM 163573, 23485, 23499, **23500**, 279241. Lanai: USNM 570736–744. Molokai: BPBM 1576, 6595, 6715–17. Maui: BPBM 11557–560, MCZ R1093, R174988. Oahu: BMNH 1903.2.21.5–7, BPBM 0863–64, 6158, 6567, FMNH 42251, 212245, USNM 23509, 58969, 59482, 59493–496, 59722–723, 279238–240.

POLYNESIA [POLYN]. Cook Islands, Mangaia: SDNHM 67822–824. French Polynesia, Marquesas: BMNH 1926.1.20.38, 1926.1.20.50, FMNH 17914, MNHN 1988.3034; Society Islands: MNHN without number, USNM 68047. Henderson Island: BMNH 1913.1.17.1–17.3.

FIJI AND TONGA [FIJI]. Vanua Levu: AMS R107894, USNM 322442; Viti Levu: AMNH 41689, BMNH 1938.8.2.7, QM J048853, J048898, USNM 230185, 267928, 267978–979, 310810–814, 345104, WmBeckon 80–82, 148, 169, 173, 175. Samoa: USNM 345102. 'Eua: USNM 268045–046, 322119; Tongatapu: CAS 49971, USNM 268044, 322120; Vava'u: USNM 333617; Tonga-Ata: BMNH 91.11.13.1.

NEW CALEDONIA AND VANUATU [NCAL]. New Caledonia: AMS R125697, R125699, R125787–788, BMNH 71.4.16.30A–B, 85.11.16.8, CAS 172739, MNHN 1887.270, NMB 6978. Vanuatu: FMNH 69613, ZSM R110.

TAIWAN AND JAPAN [TAIWAN]. Ryukyu Islands: KUZ 018095–096. Taiwan: CM 118859, KUZ 009612, USNM/field 123689, USNM 291710–712, 291807–810.

PHILIPPINES [PHILIP]. Palawan: CAS-SUR 28692–696, FMNH 52003, MCZ R150339. Saub: MCZ R26082.

NEW GUINEA AND SOLOMON ISLANDS [NGUIN]. New Guinea: AMNH 59045, 95887, 100200–206, CAS 192984, 192986–987, MCZ R49273, R140954–140955, R145981, USNM 119246, 203865. Solomon Islands: MCZ R79198, USNM 287441.

ISLANDS OF INDONESIA AND MALAYSIA [SUNDA]. Malaysia: KUZ 18094, MCZ 43480, 140968. Singapore: BMNH 96.6.25.11, ZRC 2.2291, 2.3282, 2.3378, 2.3469, 2.5361, 2.5385–86, 2.5415–16, 2.5622, 2.6021–22, 2.6596. Borneo: BMNH 912287, 1959.115A–B, FMNH 63661–662, 138545, 158734, 196268A, 213665, 239661, 243789, KUZ 8732, 8746, MCZ R43478, USNM 313965, ZMB 11355, ZRC 2.5671–72, 2.5675–78, 2.5955. Sumatra: BMNH 91.10.27.2, 1931.5.5.2, **1946.8.30.83**, MCZ R38971, NMW 179171, RMNH 4172 (3), 7161, SMF 23125, 30326, ZMA no number (3). Java: BMNH 85.12.3.17, NMW 179172, RMNH 28008–014, SMF 8930, 22611, USNM 44202, ZMB 31280, ZRC 2.1392. Bali: SMF 23126, WAM 109012. Komodo: UF 28878**, 28985**. East Indies: RMNH 3991.

SOUTHEAST ASIA [SEASIA]. Thailand: ZRC 2.5367.

INDIA AND SRI LANKA [INDIA]. Sri Lanka: BMNH **74.4.29.1326**, 90.11.8.5, 1908.7.2.1, 1910.3.16.4, 1972.2108, NMB 8552.

MASCARENES [MASCAR]. Mauritius: BMNH 1926.1.20.38, 1926.1.20.50, IRSN 24309, MCZ R51642–643, USNM 149760, 565090–093, ZFMK 25350, ZMA 14717, 14766. Rodriquez: BMNH 1975.416.

Hemiphyllodactylus aurantiacus

INDIA AND SRI LANKA [INDIA]. India: BMNH 74.4.29.1332, **74.4.29.1333**, 74.4.29.1334–1337, 91.11.27.1–3, 94.8.30.2, NMB 2900, 9682, NMW 14753, ZMB 10233, ZRC 2.4601, 2.4678–680.

Hemiphyllodactylus ganoklonis

REPUBLIC OF PALAU [PALAU]. Babeldaob: SAM R47715, USNM 495065–066, 563663–666. Ngeanges: USNM 563667. Ngeaur: USNM 563668.

Ngercheu: USNM 563669–674. Ngerekebesang: USNM 563675. Ngeruktabel: USNM 563676. Oreor: USNM 563677. Ulebsechel: USNM 563678–681, **563682**, 563683.

Hemiphyllodactylus harterti

ISLANDS OF INDONESIA AND MALAYSIA [SUNDA]. Malaysia: BMNH **1901.3.20.2**, ZMB **15360**.

Hemiphyllodactylus insularis

PHILIPPINES [PHILIP]. Bohol: CAS-SU 25107. Borocay: CAS 127889, 127965–971. Cancuman: MCZ R26600. Cebu: CAS-SU 27310, 125228, 132632, 136844, 138320, 145922–929, CAS-SU 28451, 28602. Great Govenen: CAS 60605. Mantique: CAS-SU 28987. Mindoro: BMNH 26085, CAS 62065, CM **2052,** 2053, MCZ R26084, R26601, ZMA no number. Negros: AMNH 86598–599, 115512, BMNH 1976.1681, CAS 131795, 137652, 137654, 137659, 156017, 156019, 185989, CAS-SU 19373–374, 24832, MCZ 37700, RMNH 18009, USNM 310791–793. Palawan: CAS 139142, MNHN A951. Panay: CAS 137581–583. Poro: CAS 124517–518. Semirara: CAS 127855–857. Siquijor: CAS-SU 26450, 26597–607. Tabalas: CAS 137203–206, MCZ 26083.

Hemiphyllodactylus margarethae

ISLANDS OF INDONESIA AND MALAYSIA [SUNDA]. Sumatra: AMS R129492, BMNH 91.9.24.9, IRSN 2375A–B, RMNH 7341 ZMA no number (1), **11095**, 11096.

Hemiphyllodactylus titiwangsaensis

ISLANDS OF INDONESIA AND MALAYSIA [SUNDA]: Malaysia: AMS R135270, MCZ R166921, ZFMK 32284–286, ZRC 2.4780–81, **2.4782,** 2.4783–85, 2.4832, 2.1565, 2.5419, 2.5942–5943.

Hemiphyllodactylus yunnanensis

CHINA [CHINA]. Myanmar: BMNH 1933.7.8.11, USNM 310819, 570732–735. Yunnan: BMNH **1904.1.26.1**, 1904.11.29.1–9, 1904.11.29.10A–N, CMS 8153, FMNH 7716–17, MCZ R18967, MNHN 1912.293, 1912.295A–B, 1912.296, NMB 9541. Laos:

FMNH 14451–452. Thailand: BMNH 1931.11.21.1, BPBM 3502, FMNH 178328, 180867, 215988–994, QM 4820, THNHM 0153–54, 5943–949, USNM10621–622, 310798–808. Vietnam: MNHN **1948.43**–44, RMNH 28007, USNM 310797.

Hemiphyllodactylus "yunnanensis"

Southeast Asia [SEAsia]. Cambodia: FMNH 270569. Thailand: THNHM 075, 4714–715, 4910–17, 8620, ZRC 2.3567. Thailand, country only: BPBM 3502 hermaphrodite with large testes and pair of vitellogenic follicles (diameter 3.2 mm). Vietnam: USNM 146161.

Hemiphyllodactylus [species indeterminate]

Islands of Indonesia and Malaysia [Sunda]. Borneo: Brunei: ZRC 2.5672, 2.5675–78; Kalimatan: KUZ R8723, R8746, USNM 313965; Sabah: BMNH 95.9.11.5A&B, 1929.12.22.87, FMNH 63661–662, 239661, 243789, MCZ R43478; Sarawak: FMNH 138545, 158734, 196268A, 213665, ZRC 2.5671, 2.5955.

China [China]. Hong Kong: MCZ R182874–876, MNHN 1912.293.

India and Sri Lanka [India]. Sri Lanka: BMNH 91.03.16.4, NMB 8552.

TYPE SPECIMENS

Catalog numbers for the primary type specimens here are identified in **bold** in the preceding locality samples.

Hemiphyllodactylus typus Bleeker: BMNH 1946.8.30.83.

Hemidactylus aurantiacus Beddome: BMNH 74.4.29.1332–1337, ZMB 10233.

Spathodactylus mutilatus Günther: BMNH 1946.8.30.83.

Lepidodactylus ceylonensis Boulenger: BMNH 74.4.29.1326.

Hemiphyllodactylus leucostictus Stejneger: USNM 21220, 23459–460, 23485, 23499–500, 23509.

Lepidodactylus Harterti Werner: ZMB 15360.

Gehyra larutensis Boulenger: BMNH 1901.3.20.2.

Gehyra yunnanensis Boulenger: BMNH 1904.1.26.1–26.2.

Hemiphyllodactylus insularis Taylor: CAS 62065, CM 2052–53.

Hemiphyllodactylus margarethae Brongersma: ZMA 11095–096, IRSN 2375A–B.

Hemiphyllodactylus typus chapaensis Bourret: MNHN 1948.43–44.

Hemiphyllodactylus typus pallidus Auffenberg: UF 28878, 28985.

Hemiphyllodactylus ganoklonis Zug: SAM R47715, USNM 495065–066, 563663–683.

Hemiphyllodactylus titiwangsaensis Zug: ZFMK 32284–286, ZRC 2.4780–4785, 2.4832, 2.1565, 2.5419, 2.5942–5943.

ADDITIONAL LOCALITY RECORDS

The following localities derive from distributional records appearing in publications and from museum specimen records for specimens that I did not examine directly. The specific identity provided by the museum or in the publication is the one usually followed; however, where information was adequate and contrary to author's species determination, I have re-identified the specimen.

Hemiphyllodactylus typus

Mascarene Islands. La Réunion: Déso et al. (2007); Rodriques: Schröder and Röll (2004).

Nicobar Islands. Great Nicobar Island: Biswas and Sanyal (1980).

Sumatra. Pulau Enggano: MVZ 39345–39346, 239586.

Thailand. Kanchanaburi, Nakhon Ratchasima, Narathiwat, Phang-Nga, Phuket, Ranong, Trang, and Trat provinces: Pauwels and Sumontha (2007).

Vietnam. Southernmost mapped locality: Bobrov and Semenov (2008).

China. Hainan Island: MVZ 42817–42818.

Ryukyu. Iriomotejima: Ota (1990).

Taiwan. Main island: Ota (1989).

Papua New Guinea. Milne Bay Province, Pini Range: Kraus and Allison (2004).

Solomon Islands. Guadalcanal: McCoy (2006).

Hawaiian Islands. All major islands: McKeown (1996).

Marshall Islands. Enewetak: R. I. Crombie (unpublished manuscript, "Pacific amphibian and reptile distributions," 1994).

Cook Islands. Rarotonga: Gill (1998).

French Polynesia. Marquesas: Elao, Hivo Oa, Mohotani: Ineich and Blanc (1989); Pitcairn: Ineich (1992); R. I. Crombie (unpublished manuscript, 1994).

Hemiphyllodactylus aurantiacus

India. Anaimalai Hills, Bangalore, Kolli Hills, Nilgiri Hills, Shevaroy Hills: Bauer and Das (1999);

Bangalore: Daniels (1994); Andhra Pradesh, Visakhapatnam District, Araku Valley and Madhygulu: Sanyal et al. (1993).

Hemiphyllodactylus yunnanensis

CHINA. Yunnan–Changyuan, Chengjiang, Chuxiong, Gejiu, Jinping, Lijang, Longling,Yao'an; Guizhou–Anlong, Dushan, Huishui, Xingyi; Guangxi–Dayaoshan: Zhou et al. (1981).

VIETNAM. All mapped localities N of 15°N: Bobrov and Semenov (2008, op. cit.); Tam Dao: MVZ 226500.

Hemiphyllodactylus "yunnanensis"

CAMBODIA. Phnom Tumpor: Grismer et al., (2008); Koh Rongnieur and Koh Khlee-Ay islands, Megong R.: Bezuijen et al. (2009).

THAILAND. Khao Yai National Park: Chan-ard et al. (1999).

Hemiphyllodactylus [species indeterminate]

(THESE LOCALITIES NOT MAPPED)

SRI LANKA. Southwestern Sri Lanka: Somaweera and Somaweera (2009).

Appendix 3: Statistical Analyses

Ised standard univariate statistics to summarize variation of the characters within each sample. These data are the main ones presented for the comparison and description of samples, the means for mensural data, and the medians for meristic data. I tested all samples with adequate numbers of adult females and males for sexual dimorphism with the Student t test, significance at $P \leq 0.05$. A repeats protocol provided an estimate of the variation derived from my data gathering (see detailed explanation in Baseline Estimate of Intra-Observer Variation subsection).

Multivariate statistics (discriminant function analysis [DFA] and principal components analysis [PCA]) were used mainly to explore the homogeneity of samples. My goal was to discover which mensural traits best differentiated between unisexual and bisexual individuals within large regional samples. I did not use scalation traits in these analyses, although I did use proportions in some analyses but did not mix measurements. Some authors (e.g., Atchley et al., 1976) have argued against the use of proportions in multivariate tests and demonstrated problems with proportional data through simulation studies. Other authors have shown that proportions and nontransformed measurements do not yield significantly different results in data sets from museum specimens such as frogs (Heyer, 1978) and turtles (Iverson, 1981). I justify my use of proportions herein because I was neither testing differences between or among groups or relying on statistical significance in the assignment of specimens to taxonomic group.

The following paragraphs present a synopsis of the statistical results from the comparison using PCA and DFA. They are arranged in the same sequence as in the text.

Uniformity among the unisexual samples: A DFA was employed to test uniformity (homogeneity) of the adults ($n = 119$) of the Pacific samples including the holotype of *H. typus* using the eight mensural traits (EyeD, HeadL, HeadW, NarEye, SnEye, SnW, SVL, TrunkL; TailL was not examined in this test nor any of the subsequent ones). The adjusted classification matrix (jackknifed) yielded an average accuracy of 23% assignment. The first three predictor variables (SVL, TrunkL, HeadL) had eigenvalues of 0.373, 0.317, and 0.180 and accounted for

36.5%, 31.0%, and 17.6% of the total variance, respectively. A PCA (covariance matrix) of the same combined samples and traits produced a compact clustering on the first two components. The first three components had eigenvalues of 24.72, 1.064, and 0.156, respectively, with the first component accounting for 94.6% and the second component 4.1% of total variance. SVL, TrunkL, and HeadL had the strongest loading (eigenvalues of 0.826, 0.534, and 0.131).

Principal components analysis of body proportions in SUNDA *sample:* Principal components analysis (correlation matrix) results for adult females (*n* = 72) are summarized in the text with the exception of eigenvalues for the first four components: 2.712, 2.400, 1.639, 1.206; these components accounted for 79.7% of total variance. A PCA of adult males (*n* = 9) identified HeadL/SVL and SnW/HeadW as the highest loading variables on the first component, NarEye/HeadL on the second, TrunkL/SVL on the third, and SnW/HeadL on the fourth. In total, these four components accounted for 91% of total variance, with 48.1% for the first component. Eigenvalues for the first four components were 4.826, 2.567, 0.948, and 0.826. Dispersion on a plot of first and second components was broad, although a regional clustering occurred with Sumatran males in the upper left quadrant, Bornean males in the lower third of the upper right quadrant, and Malaysian males in the lower left quadrant.

Discriminant function analysis examination of INDIA *sample:* A DFA of INDIA males (*n* = 6 India, 1 Sri Lanka) yielded 71% accuracy (jackknifed classification) using eight mensural traits and a considerably lower accuracy (14%) with the 10 proportional traits. The accuracy for the unadjusted classification was 100% for both character sets. The eigenvalues for the two analyses were 13.073 and 7.029, respectively. Using the 10 proportional traits, classification accuracy was better (80% jackknifed) in the adult females (*n* = 4 India, 1 Sri Lanka); mensural traits were not examined in females.

Discriminant function analysis examination of Malaysian Hemiphyllodactylus samples: The distinctiveness of the *H. harterti* sample (*n* = 2 adults) and a central mountain range sample (15 adults) was explored with two data sets, the eight mensural traits, and a subset of eight meristic traits (CircNa, SnS, Suplab, Inflab, Chin, CloacS, Subcaud, TotPore). The latter subset had been identified as the best set of discriminators by an earlier DFA of all 22 scalation characters. Of the mensural set, HeadL, SnEye, and OrbD were assigned the largest classification functions. The unadjusted classification matrix yielded 100% accuracy of group assignment and the jackknifed matrix only 76% total accuracy, with a single eigenvalue (3.045) reported. The meristic set yielded 100% classification accuracy in the unadjusted matrix and 94% in the jackknifed matrix, with a single eigenvalue (13.241) reported.

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Index of Taxa Names

Page numbers in **bold italic font** indicate the start of the taxonomic account.

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