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THE *SPHAERODACTYLUS* (SAURIA: GEKKONIDAE)
OF MIDDLE AMERICA

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INTRODUCTION

Sphaerodactylus is one of the most speciose genera of gekkonid lizards. It is confined to the Neotropics, and the majority of its diversity is found in the West Indies where approximately 69 species, and an additional 74 subspecies, have been well-documented (King, 1962; Schwartz, 1964, 1966, 1968, 1977; Schwartz and Garrido, 1981; Schwartz and Graham, 1980; Schwartz and Thomas, 1964, 1975, 1983; Schwartz, Thomas, and Ober, 1978; Thomas, 1964, 1975; Thomas and Schwartz, 1966a,b). The mainland radiation was poorly understood until 1982 when Harris published his revision of South American sphaerodactyls. No comprehensive study has yet been attempted for Middle American forms, and it remains the last area of taxonomic confusion in the genus. The number of taxa currently recognized in Middle America is not great (10 species according to Peters and Donoso-Barros [1970], Schwartz [1973], and Smith and Taylor [1950b, 1966]); however, their geographic distribution and variation, and status as species or subspecies remain to be convincingly demonstrated.

The Middle American sphaerodactyl fauna appears to be divisible into two geographical-historical components. Most of the taxa may be thought of as belonging to an endemic group because the sister taxon

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of each species also exhibits a mainland distribution. Only two, *S. argus* Gosse (1850) and *S. rosaurae* Parker (1940), belong to widespread West Indian species or species-groups. The mainland distribution of *S. argus* is largely coastal and on off-shore islands, where it exhibits no obvious differentiation from presumed conspecifics in the West Indies. *Sphaerodactylus rosaurae* is restricted to the Islas de la Bahía of Honduras, but it is considered a member of the Greater Antillean "*copei*" species-group (Schwartz and Garrido, 1981).

Other Caribbean sphaerodactyls, *S. anthracinus*, *S. cinereus*, *S. fantasticus*, and *S. sputator*, have been reported from Middle America. In fact, Cope (1862a:500) claimed that the holotype of *S. anthracinus* was from "Mexico," and Günther (1885–1902) restricted its origin to Jalapa (Veracruz was added later by Schwartz and Thomas, 1975). However, Barbour (1921:258) found the male holotype (ANSP 7558, not "types" as per Taylor [1947]), "to be absolutely identical with examples from Andros Island in the Bahamas," which were the syntypes of *S. asper* (MCZ 6222), and he concluded that the mainland locality "is certainly erroneous." Wilhelm Peters' (1869) record of *S. anthracinus* from Puebla was overlooked by Barbour (1921), and it may give credence to a mainland origin for the species (Parker, 1940). Boulenger's (1885) specimen from San Domingo, West Indies was incorrectly interpreted by Taylor (1947) to be from México. Thomas (1968) regarded *S. anthracinus* as a *nomen dubium* because of its unicolor pattern which is unlike that of any other Antillean sphaerodactyl, its questionable geographic origin, and because similar specimens have not been retaken from Andros Island. The Antillean populations which had been referred to *S. anthracinus* (Schwartz, 1961) have come to be called *S. copei* by Schwartz and Thomas (1964) and Thomas (1968) though it is not apparent that either author examined the type of *S. anthracinus*. The three other species said to have been collected in México appear not to have been retaken there since the original references: *S. cinereus* (Troschel, 1865), *S. fantasticus* (Hallowell, 1861), and *S. sputator* (Cope, 1865). All of these seem to be based on erroneous geographic attributions or misidentifications.

The following 14 names have been given to the Middle American endemics: *S. carinatus* Andersson (1916), *S. casicolus* Cope (1862a), *S. continentalis* Werner (1896), *S. dunni* Schmidt (1936), *S. glaucus* Cope (1865), *S. homolepis* Cope (1886), *S. imbricatus* Andersson (1916), *S. inornatus* W. Peters (1873), *S. lineolatus* Lichtenstein and von Martens (*in* Lichtenstein, 1856), *S. mertensi* Wermuth (1965), *S. millepunctatus* Hallowell (1861), *S. pacificus* Stejneger (1903), *S. rosaurae* Parker (1940), and *S. torquatus* Strauch (1887). The names *S. casicolus*, *S.*

homolepis, and *S. lineolatus* have also been applied to South American populations (Harris, 1982).

In the present study we review those sphaerodactyls found on mainland Middle America. The highly distinctive, insular *S. rosaurae* and *S. pacificus* (Isla del Coco, Costa Rica) are only treated in the diagnostic key to the species (pp. 50–51).

METHODS AND MATERIALS

We follow Harris' (1982) character and character state definitions to insure the comparability of the two revisions. These usages do not entirely conform to studies on Caribbean sphaerodactyls, and we redescribe those characterizations that are especially different. Dorsal scales were counted middorsally, between the axilla and the groin, with the limbs extended laterally from the body (the count was not made dorsolaterally). The internasal count is the minimum number of scales separating the supranasals, which does not necessarily also include those in contact with the rostral. Interorbital width (IOW), or the shortest distance across the frontal bone, was used to standardize scale sizes. Three IOW means that a diagonal series of three scales is as wide as the narrowest part of the frontal bone. The snout angle is a measurement of the convergence of the sides of the snout, as viewed dorsally. The angle cannot be determined for all specimens because snout shape is affected by different methods of preservation. Adult males were distinguished on the basis of an escutcheon (hypertrophied subfemoral and/or abdominal scales). Equally large specimens lacking an escutcheon were considered to be females.

In the lists of specimens examined, we have freely altered invoice data to reflect generally accepted form and spelling of place names. In some instances comments and reinterpretations appear in brackets. The following abbreviations are used to denote the sources of the material we examined.

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
ASFS	Albert Schwartz Field Series
BMNH	British Museum of Natural History
CAS	California Academy of Sciences
CAS-SU	Stanford University Collection at CAS
CM	Carnegie Museum
CRE	Costa Rica Expeditions; formerly at University of Southern California, now at University of Miami
EAL	Ernest A. Liner, personal collection
FMNH	Field Museum of Natural History
GML	Gorgas Memorial Laboratory
GNM	Göteborgs Naturhistoriska Museum
ICN	Instituto de Ciencias Naturales, Universidad Nacional, Bogotá
INDR	Instituto de Recursos Naturales Renovables y del Ambiente, Bogotá
KU	University of Kansas Museum of Natural History
LACM	Los Angeles County Museum of Natural History
LSUMZ	Louisiana State University Museum of Zoology

MCZ	Museum of Comparative Zoology, Harvard University
MPM	Milwaukee Public Museum
MVZ	University of California at Berkeley, Museum of Vertebrate Zoology
RT	Richard Thomas, personal collection
TCWC	Texas Cooperative Wildlife Collection, Texas A&M University
UCM	University of Colorado Museum
UCR	Universidad de Costa Rica
UF	Florida State Museum
UIMNH	University of Illinois Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
USNM	National Museum of Natural History, Washington, D.C.
UTACV	University of Texas at Arlington, Collection of Vertebrates
UTEP	University of Texas at El Paso
ZIN	Zoological Institute of the Academy of Sciences of the USSR, Leningrad
ZMB	Universität Humboldt, Zoologisches Museum

We have attempted to include all literature references in the species synonymies. Minor taxonomic spelling variations (e.g., *Sphaeriodactylus*) have not been listed separately.

SPECIES ACCOUNTS

Sphaerodactylus graptolaemus n. sp.

Figs. 1A, 2, 16, 18

Sphaerodactylus lineolatus—Bocourt (1873:46), Savage (1980:77).

Sphaerodactylus lineolatus (part)—Taylor (1956b:40).

Sphaerodactylus sp.—Taylor (1956b:53).

Sphaerodactylus continentalis (part)—Savage (1973a:10).

HOLOTYPE: UCR 3592, an adult male collected on 4 May 1970 by Ricardo Rivera.

TYPE-LOCALITY: COSTA RICA: PUNTARENAS; Isla del Caño.

PARATOPOTYPES: UCR 3589, a juvenile collected on 5 May 1970 by Ricardo Rivera, and UMMZ 174004, an adult female, collected on 23 Feb. 1970 by D. C. Robinson and R. Saenz C.

ETYMOLOGY: Most of the specimens have distinctive lines on the throat (Fig. 2). It is for this diagnostic aspect of the color-pattern that the species is named *graptolaemus* (Greek).

DIAGNOSIS.—A moderately large sphaerodactyl, males attaining 29.4 and females 31.7 mm. snout-vent length (SVL). Dorsal trunk scales moderate in size, homogeneous, keeled, 51–63 between axilla and groin. Ventral count 32–37, averaging 59.3% of dorsal count. Scales around midbody 67–83. Parietal granules keeled. Supranasal single, large, separated medially by one or rarely two internasals.

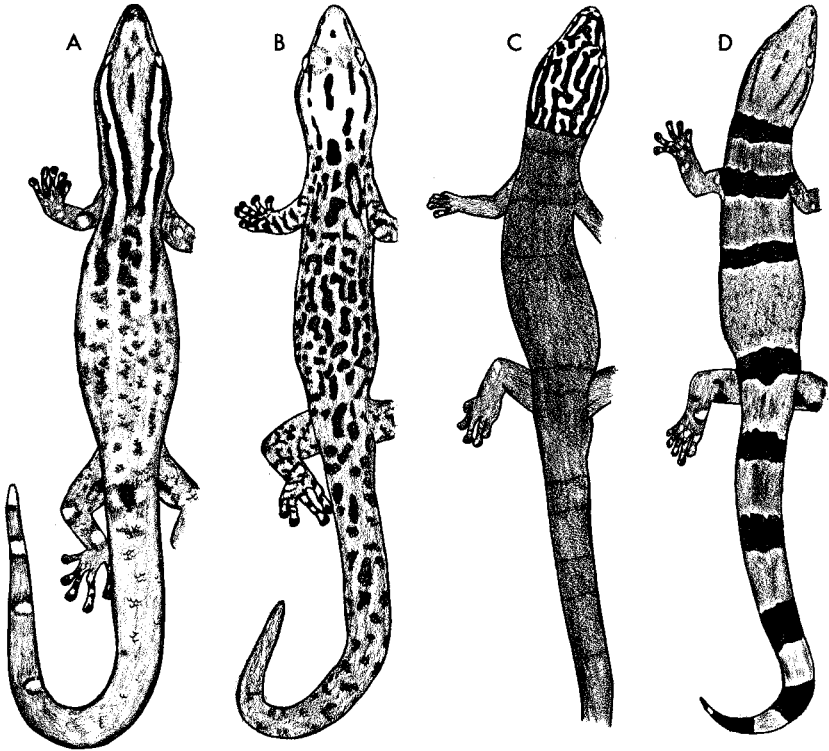


FIG. 1. Color-patterns of (A) *Sphaerodactylus graptolaemus* (composite: UMMZ 174004, female, and tail tip from CAS 65892), (B) *S. lineolatus* (UMMZ 124889, male), and (C–D) *S. homolepis* (GNM 1326c, male; GNM 1325, female). Drawn by D. M. Harris.

Rostral with long median cleft, small posterior notch intruded by part of a small scale. Fourth supralabial lies below anterior half of eye; fourth infralabial below center of eye. Subcaudal scales enlarged, 3–4 times width of supracaudals; aligned in a median series. Escutcheon consists of 22–61 scales, elliptical or roughly triangular in shape, with base toward vent but not extending onto thighs. Males like females in coloration (in preservative) with dark-bordered, light dorsolateral bands extending from eye to trunk, then changing into dark spots, which in turn become fewer on tail; end of tail with light cross-bands; throat with dark lines curving toward midline.

Sphaerodactylus graptolaemus may be distinguished from *S. lineolatus* and *S. homolepis* by the continuous row of median subcaudal scales, and from *S. lineolatus* also by having a lower dorsal count. *Sphaerodac-*

tylus graptolaemus differs from *S. millepunctatus* and *S. argus* by having a single supranasal per side. Unlike *S. graptolaemus*, *S. glaucus* has smooth scales and two supranasals; *S. dunni* has large body scales and alternating median subcaudals. The *S. graptolaemus* color-pattern, dark-bordered dorsolateral light stripe from eye onto trunk and throat stripes, is approached by some specimens of *S. millepunctatus*; otherwise it is unique among Middle American sphaerodactyls.

DESCRIPTION.—UCR 3592, 3589, and UMMZ 174004, respectively. A moderately large sphaerodactyl, 28.0, 16.1 and 31.7 mm. SVL. Snout-ear distance 7.0 mm., head length 4.2 mm. and head width 3.4 mm. in UMMZ 174004. Snout moderately long, its length equals distance from ear to posterior third of eye. Sides of snout converge at angles of 40°, 48° and 42°; tip rounded.

Rostral with long median cleft, small posterior indentation intruded by part of one small scale. Supranasal single. Postnasals one or two. Space between supranasals narrower than supranasal scale width. Internasal single. Snout scales flat, keeled, juxtaposed; nine, ? and 10 from orbits. Parietal surfaces and nape with keeled granules; 6–7 per IOW, fourth supralabial lies below anterior half of eye; fourth infralabial below center of eye; first infralabial largest, its length equals 1.5 IOW. Mental large, its rear border with forward slanting lateral edges. Postmentals polygonal, slightly elongated; two border mental. Gular scales smooth, granular, about six per IOW.

Dorsal scales of trunk oval, flat, keeled, imbricate, four per IOW; 51, 58 and 63 along middorsum between axilla and groin. No zone of middorsal granules. Lateral scales like dorsals. Ventrals round, thin, smooth, imbricate, two per IOW; 33, 36 and 37 axilla-groin. Ventral counts 58.7–64.7% of dorsal counts. Scales around midbody 75, ? and 77. Escutcheon of holotype five scales long and nine wide, about 29 total.

Supracaudals rhomboid, flat, imbricate, keeled at tail base (for a head length), smooth distally; in diagonal and transverse series; 2.5 per IOW. Subcaudal scales smooth, four times wider than supracaudals, though not transversely expanded; forming a continuous median series. Male may have about six swollen granules lateral to vent. Limb squamation similar to that of trunk. Digit scales keeled, imbricate, 14, 11 and 13 lamellae below fourth toes.

The preserved male, female (Fig. 1A) and juvenile do not differ substantially in color. Tan with fine dark brown (raw sienna) markings. A bold cream stripe with dark edges extends from eye to tail; dark edge breaks up on trunk, forming series of spots. Dark streaks on canthus and longitudinally between eyes and occiput. Dark spot over pelvis, flanked by light-centered ocelli. Additional streaks begin

at eye and corner of mouth and run below and on side of neck. Infralabials blotched with brown; center of throat and other underparts light, immaculate. Limbs with prominent light-centered ocelli and light postfemoral bar edged with black, extending slightly onto tail base. These ocelli are particularly distinct in the juvenile (UCR 3589). One ocellus actually occurs on body just anterior to forelimb insertion. Others on forelimb appear over elbow and on rear surface of forearm. Hindlimb ocelli are situated dorsal to femur and knee, and in front of and behind foreleg. Digits banded above.

VARIATION.—Ten mainland specimens are referred to *S. graptolaemus* and, combined with the types, form the following summary (N=13, unless otherwise indicated). Males appear smaller than females, 24.3–29.4 mm. SVL (\bar{x} =27.3, s =1.56, N=7) and 28.2–31.7 mm. SVL (\bar{x} =30.2, s =1.79, N=4), respectively. Snout-ear distance 19.1–24.3% of SVL (\bar{x} =22.4, s =1.6, N=9). Head width 57.1–74.1% (\bar{x} =63.2, s =5.9, N=9) and head depth 40.9–50.0% (\bar{x} =44.9, s =3.4, N=9) of snout-ear distance. Sides of snout converge at 40–48° (\bar{x} =43.0, s =2.84, N=11). Complete original tail 108% of SVL in CAS 65892. Fourth supralabial divided in two specimens. Dorsal scales (axilla-groin) 51–63 (\bar{x} =58.2, s =3.69); ventral counts 32–37 (\bar{x} =34.4, s =1.80), 53.3–66.1% of dorsal counts (\bar{x} =59.3, s =4.5). Scales around midbody 67–83 (\bar{x} =75.3, s =4.52, N=12). Lamellae under fourth toe 11–16 (\bar{x} =12.9, s =1.32, N=12 pairs). Escutcheon may reach groin, 5–8 by 6–10, a total of 22–61 scales (\bar{x} =36.7, s =12.5, N=7). Color pattern varies little; in some specimens the chin is mottled. Sometimes another dark gular streak is discernable as in fig. 2.

Only one juvenile and one adult have complete original tails. The tail is generally spotted more intensely at the base, but toward its terminus it is crossed by four light, dark-bordered spots or rings.

DISTRIBUTION.—Southern Pacific versant of Costa Rica and adjacent western Panamá.

REMARKS.—Historical circumstances require that we justify why the name *S. lineolatus* cannot be applied to the species we are calling *S. graptolaemus*. *Sphaerodactylus lineolatus* was based on three syntypes (“stuck 3”), however, according to Günther Peters (pers. comm.): “In the general catalogue of [ZMB] under the number 417, four specimens of *S. lineolatus* are noted by Lichtenstein. Three of them much later had been transferred by Wermuth to number 36297.” We have identified three of the specimens as belonging to the same species, *S. lineolatus*, but the fourth, ZMB 36297a, appears to be of *S. graptolaemus*.

There are two claims regarding the designation of a lectotype of *S.*

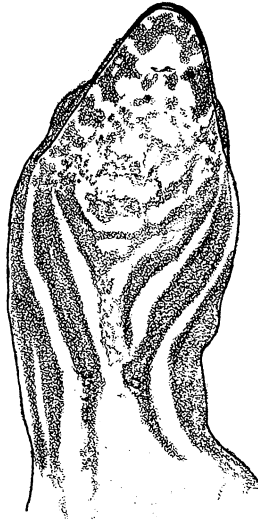


FIG. 2. Pattern on the underside of the head and neck of *Sphaerodactylus graptolaemus* (MCZ 128517). Drawn by D. M. Harris.

lineolatus. The first reference to a singular type-specimen was that of Dunn (1940:189): "... I have examined the type of [*S.*] *lineolatus* Lichtenstein and Martens (Berlin 417) from Veragua." Dunn did not use the term lectotype; however, his action may be thought to be precedent setting because it prompted Wermuth to recatalogue part of the series. Stuart (1963:56) later called ZMB 417 the lectotype of *S. lineolatus* "fide H. Wermuth (*in litt.*)." Alternatively, Taylor (1956b:41) stated: "I designate this specimen redescribed by Bocourt as the type (lectotype) of the species [*S. lineolatus*]." Bocourt's (1873:46) specimen was said to have had lines on the head, which disappeared at the beginning of the sides, and a series of large scales below the tail, characters that correspond best to the exceptional specimen, ZMB 36279a, although it is now missing its tail. Our recognition of the species to which ZMB 36297a belongs is based principally on dorsal scale size—color pattern is obscure in all the specimens and one other specimen is missing its tail as well. Therefore, it is only by weak inference that we are able to assume which specimen is Taylor's "lectotype."

Differences between Lichtenstein and von Martens' description of *S. lineolatus* and Bocourt's "redescription" suggest that Lichtenstein and von Martens probably did not use 36297a. Lichtenstein and von Martens' three specimens had backs which were dark-vermiculated,

and the lines on the head were not noted as continuing onto the anterior trunk. Bocourt's description did not mention any dorsal pattern except for the lines of the head disappearing at the beginning of the sides. It is our contention, then, that the specimen seen by Bocourt was not of the type-series, and therefore Taylor's "lectotype" is an inappropriate representative of Lichtenstein and von Martens' *S. lineolatus*.

We conclude that Dunn (1940) effectively designated the lectotype of *S. lineolatus* of Lichtenstein and von Martens and that Taylor's (1956) subsequent designation of a lectotype was confusing because the identity of the specimen could only be surmised inferentially, but moreover was invalid because the designated specimen in our estimation is not a syntype. Two advantages are derived by accepting Dunn's action. First, we do not need to assume misprints in the literature. ZMB 417, perhaps originally a lot of four specimens, may well have been catalogued after the description of *S. lineolatus*. Secondly, our conclusion preserves the stability of nomenclature, a paramount objective of the Internal Code of Zoological Nomenclature (1961:3).

REFERRED SPECIMENS.—COSTA RICA: PUNTARENAS: Golfito (MVZ 79787); Golfito, 0 m. (KU 66856); 5 km. S Finca Los Angeles (UCR 2503); Finca Ojalá, 1 km. SE Puerto Quepos, 100 m. (CRE 4421); Rincón de Osa (MCZ 128517); ca. 2.5 km. SW Rincón de Osa Tropical Science Center (USNM 219545); 18 km. from San Isidro del General toward Dominical (UCR 1878).

PANAMÁ: Chiriquí: Puerto Armuelles (ANSP 21777; CAS 65892). PROVINCE UNKNOWN: "Veragoa" (ZMB 36297a).

Sphaerodactylus lineolatus Lichtenstein and von Martens
Figs. 1B, 3–5, 16, 18

Sphaerodactylus lineolatus Lichtenstein and von Martens (*in* Lichtenstein, 1856:6). Type-locality: Veragoa [?= Panamá: Veraguas; Santiago de Veragua]. Lectotype: ZMB 417 (restricted by Dunn, 1940). Paralectotypes: ZMB 36297b–c. Collector: J. von Warszewicz.

Sphaerodactylus casicolus Cope (1862a:499). Type-locality: Region of the Truandó, New Granada [= Colombia: Chocó; lower Atrato River region]. Holotype: Mus. Washington [USNM—never catalogued and presumed lost (W. R. Heyer, pers. comm.)]. Collector: not stated.

Sphaerodactylus casicolus—Cope (1862b:356), Günther (1885–1902:82).

- Sphaerodactylus lineolatus*—Cope (1862a:497), Barbour (1906:225; 1921:218, 238), Schmidt (1933:8; 1936:47), Swanson (1945:212), Cochran (1946:2), Shreve (1947:523), Smith and Taylor (1950a:320), Grant (1959:199), Smith and Alvarez del Toro (1962:103), Shelford (1963:415), Smith and Terentjev (1963:367), Myers and Rand (1969:3), Schwartz (1973:142.2).
- Sphaerodactylus lineolatus* (part)—Günther (1885–1902:82), Cope (1887:27), Dunn (1940:189), Breder (1946:426), Taylor (1956b:40), Stuart (1963:56).
- Sphaerodactylus lineolatus* (unconfirmed)—Wever (1973:324, 329; 1978:468, 480, 524, 528–9, 543, 560–1).
- Sphaerodactylus homolepis*—Boulenger (1899:914).
- Sphaerodactylus pacificus* [?]
—Busack (1966:371).

DIAGNOSIS.—A moderately large *Sphaerodactylus*, males and females attaining 30 and 32 mm. SVL, respectively. Dorsal trunk scales minute, homogeneous and moderately keeled; 62–81 between axilla and groin. Ventral count 33–42, averaging 52.9% of dorsal count. Scales around midbody 74–94. Parietal granules smooth. Single large supranasal, descending behind nostril; supranasals separated medially by one small scale (Fig. 3). Rostral with long median cleft and small posterior notch containing part of a small scale. Fourth supralabial lies below anterior half of eye; fourth infralabial below center of eye. Subcaudal scales up to three times width of supracaudals; not forming continuous median series, but with repeating sequence of a single small, a single large, and a pair of small scales (Fig. 4). Escutcheon small, situated on posterior fourth of venter, not extending sub-femorally; composed of 20–52 glandular scales. Dorsum variegated in adults of both sexes; head with longitudinal lines, accentuated in males (Fig. 1B). Juveniles with broad dark brown bands (four on dorsum of trunk and nape) which become indefinite with age (may be retained as transverse rows of spots in adults).

Sphaerodactylus lineolatus can be distinguished from *S. argus*, *S. dunni*, *S. glaucus*, and *S. millepunctatus* by having one, rather than two, supranasal scales. Unlike *S. lineolatus*, the species *S. argus*, *S. graptolaemus*, *S. glaucus*, and *S. millepunctatus* have a median, continuously enlarged series of subcaudal scales. The dorsal scales of *S. homolepis* are more strongly keeled and larger than those of *S. lineolatus*; they are distinctly raised and appear knobby. Also, the dark cross-bands characteristic of juveniles become faded, but not ill-defined, in adult *S. homolepis*, whereas in *S. lineolatus* they become indefinite (i.e., with irregular edges) and are usually replaced by the variegated adult pattern.

REDESCRIPTION OF TYPE-SERIES (Male ZMB 417 and females ZMB 36297b–c, respectively).—SVL 23.8, 29.7 and 30.0 mm. Snout of

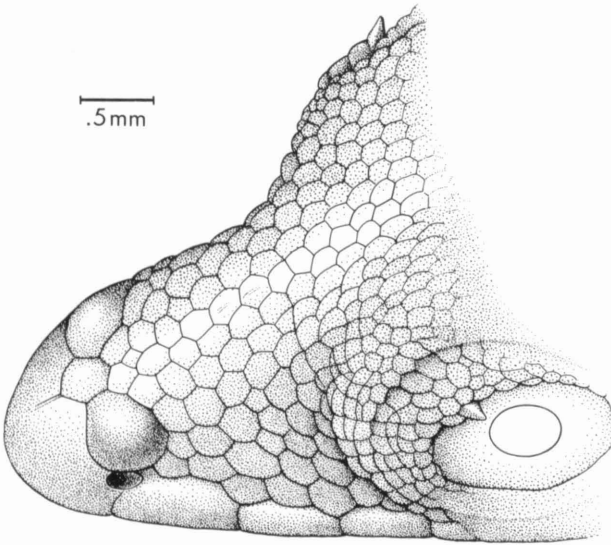


FIG. 3. Head squamation of *Sphaerodactylus lineolatus* (ZMB 36297c).

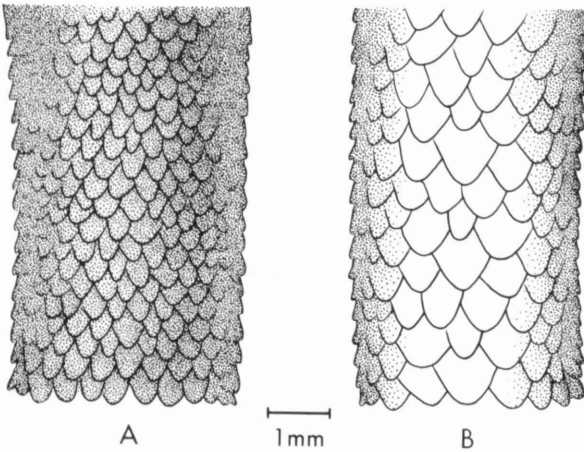


FIG. 4. Supra-caudal (A) and subcaudal (B) squamation of *Sphaerodactylus lineolatus* (ZMB 36297c).

moderate length, orbit to tip equal to distance from ear to between posterior edge and posterior third of eye. Sides of snout converge at 48°, 42° and 43°; tip rounded. The tail length was said to be equal to SVL in the original description; currently only ZMB 36297c has a complete tail 26.8 mm. long, but it is broken in two places. Rostral with long median cleft and with or without a tiny posterior indentation, containing part of one scale. Supranasals undivided, large, in broad contact with nostril, descending laterally behind nostril; separated from first supralabial by single postnasal, and from each other by single small scale. Snout scales flat, smooth, or lightly keeled, juxtaposed; nine, eleven and eight from orbits to rostral, four per IOW. Parietal surfaces and nape covered with smooth granules, 5–6 per IOW. Fourth supralabial elongate, lying below anterior half of eye. Fourth infralabial below center of eye; first infralabial largest, its length equal to 1.5–2 IOW. Mental large, as long as wide, its posterolateral borders slant forward. Postmentals polygonal, rounded, smooth, slightly swollen; two border mental. Gular scales smooth, granular, five per IOW, becoming imbricate at level of ears.

Dorsal trunk scales rhomboid, rounded, slightly swollen, faintly keeled (ZMB 36297c) or smooth (see Variation), juxtaposed, 4–5 per IOW; 71, 67 and 67 axilla-groin. Ventral scales 2–2.5 per IOW; 35, 37 and 35 axilla-groin. Ventral counts 49.4, 55.3 and 52.3% of dorsal counts. Scale rows around midbody 74, 87 and 80. Escutcheon circular, confined to posterior fourth of venter, about six scales anterior to vent; six scales long and six rows wide; total of 27 scales. Supracaudal scales rhomboid, flat, imbricate, three per IOW, smooth (keeled at base for a head length in ZMB 36297c). Subcaudal scales larger than supracaudals, those of median area largest (up to three times supracaudal width), smooth, not widened and not forming a continuous longitudinal series, but comprised of a repeating set of a single large, a single small, and a pair of small scales. Male with a cluster of one-half dozen swollen granules lateral to vent. Limb squamation corresponds to that of trunk except that scales of prefemoral surface are imbricate. Digit scales smooth, subimbricate, transversely expanded into lamellae below; 12–13 under fourth toe.

Type-specimens faded; tissues now transparent and bones stained green. Male ZMB 417 has three narrow dark lines originating at eye and disappearing on neck. These lie above a short line which runs between corner of mouth and ear opening. A dark line also runs below canthal ridge. Middorsal lines common on snout and back of head of many *S. lineolatus*; not discernible in ZMB 417. Dorsum faintly vermiculated. Venter pale and unicolor. There is a faint in-

dication of a darker collar band in the lectotype. Female ZMB 36297c has a mottled dorsum and a dark nuchal spot; ZMB 36297b is unpatterned.

Two of the type-specimens of *S. lineolatus* have unkeeled dorsal scales, while in all of the recently collected specimens examined, the dorsals are, to varying degrees, keeled. We suspect that the natural structural integrity of these scales in the two types has disappeared due to their many years in preservative, and so the smooth scale condition was not included in our diagnosis.

VARIATION.—Escutcheon size and SVL are correlated in *S. lineolatus* (Fig. 5; $r=0.284$, $N=60$, $P>0.05$). The trend is also evident in a local sample from Fort Clayton, Panamá. Interspecific differences were not examined statistically because *S. lineolatus* is markedly heteroscedastic (Fig. 5).

Ciricito, Colón, Panamá, is the *S. lineolatus* record which comes closest to the known geographic range of *S. homolepis* (Río Coclé del Norte, Bocas del Toro, Panamá; USNM 129839, a small juvenile specimen). The escutcheon totals of the two Ciricito examples (CAS 71471–72) were the largest found among Panamanian *S. lineolatus*. They (43 and 51) fall within the range for comparably sized *S. homolepis* (Fig. 5). However, the high dorsal scale counts (66 and 68), strongly variegated dorsum, smooth parietal granules, and weakly keeled dorsals are more like *S. lineolatus*. Specimens from the two *S. homolepis* localities nearest Ciricito, Río Coclé del Norte and the mouth of the Río Cahuita (KU 113101), each have dorsal counts near the high extreme for that species (66 each), which overlap the range of variation in *S. lineolatus*. While the escutcheon and dorsal scale counts suggest that the region under consideration is a zone of intergradation between two races, additional material must be collected from that area before a convincing case can be made for conspecificity.

High escutcheon counts were also found in a specimen from Islas Secas in the Pacific Ocean (47) and from Colombian material (37–42). The Islas Secas specimen also differs by having scales under the tail aligned in a median row. It is tentatively referred to *S. lineolatus* on the basis of the coloration, small size of the dorsal scales (70 axilla-groin) and moderate degree of dorsal keeling. The Islas Secas and Colombian specimens may also have keeled parietal granules, as do ANSP 23378 (Canal Zone) and FMNH 170051 (San Blas). Two other specimens were found to have a median row of subcaudals, UMMZ 135386b with four in a row and FMNH 178083 with a row running the tail length.

Color-pattern variation is discussed by Grant (1959). Adult males

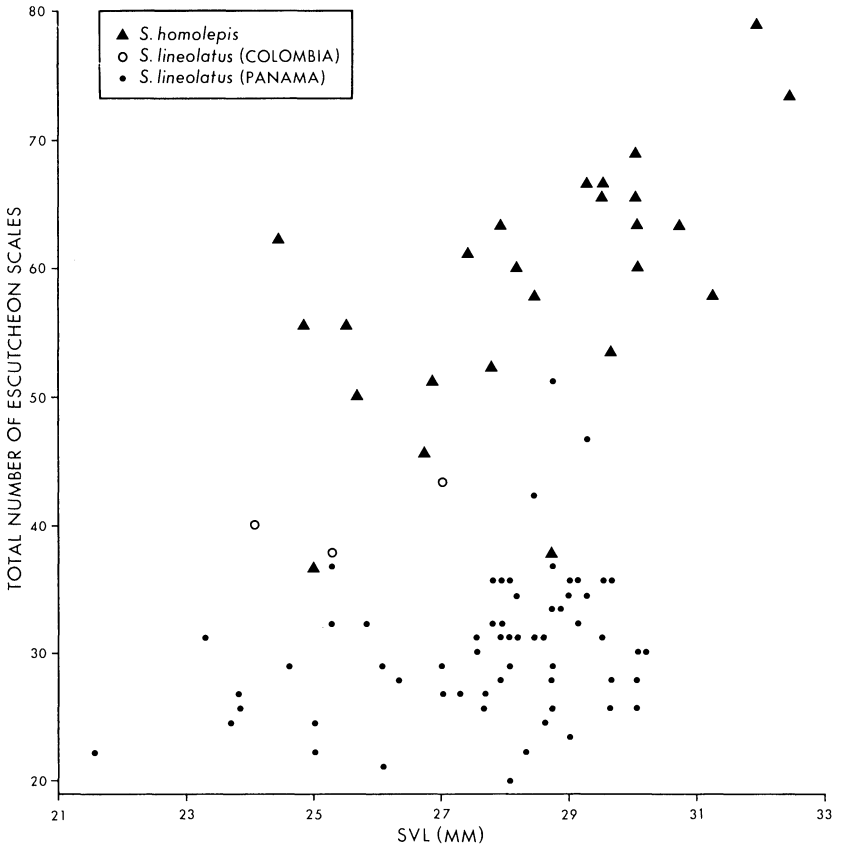


FIG. 5. Relationship between snout-vent length and escutcheon size in *Sphaerodactylus homolepis* and *S. lineolatus*.

commonly have distinct lines on the head; however, the head is virtually unadorned in some island populations (Islas Secas and Isla Saboga) and in the Curiche, Colombia specimen.

DISTRIBUTION.—Pacific-western Panamá to northwestern Colombia.

REMARKS.—Most references give Lichtenstein sole credit for the original description of *S. lineolatus*; however, he (1856:III–IV) clearly acknowledged coauthorship with von Martens: “Weinland’s Nachfolger, Herr Dr. von Martens, hat dann erst mit mir gemeinschaftlich die Redaction des Catalogs, wie er hier vorliegt, beendigen können. Wir machen uns gemeinschaftlich sowohl für die allgemeine systematische Anordnung, wie für die Nomenclatur und die in den Be-

schreibungen angewendete Terminologie verantwortlich, und. . . ." The full, correct citation is, therefore, *Sphaerodactylus lineolatus* Lichtenstein and von Martens (in Lichtenstein, 1856). Though von Martens may be considered coauthor of the species descriptions, only Lichtenstein's name is prominently displayed as author of the volume.

The place of collection, "Veragoa" [sic], of the type-series of *S. lineolatus* remains a problem. Grant (1959:202) stated that within the Province of Veragua, one of the states of New Granada, there was an area known as Veragua, which came to include "Panama City and hence the area now occupied by Fort Kobbe." He went on to state that the type-locality of *S. lineolatus* could not be accurately determined and that there is no town or specific locality bearing the name Veragua, or a permutation of it. These conclusions were supported by Smith and Alvarez del Toro (1962:103), who termed Grant's specimens from Fort Clayton (a locality approximately 10 km. N Fort Kobbe) "essentially topotypic *lineolatus*." There are several issues here, not the least of which is that the Fort Clayton material (UIMNH 46791-95) does not especially resemble the type-series of *S. lineolatus*. Moreover, there is in fact a specific locality which bore the name Veragua. In the 1880 edition of Lippincott's gazetteer of the World (p. 2301), Veragua (or Santiago de Veragua) is described as a town of 5000 inhabitants in the United States of Colombia, approximately 200 km. WSW of Panamá, near the coast. "Veragua" in that era seems to have been used in preference to Santiago (p. 1981), the name employed today for the capital city of Veraguas Province, Panamá.

Josef Warszewicz, who collected the type-series, is known to have obtained amphibians and reptiles in the region of Chiriquí and to have embarked from Panamá City for Perú (Savage, 1970). We can't be certain how he made his way between Chiriquí and Panamá City; both overland and ocean modes of travel were probably available. Warszewicz did, however, travel overland between Guatemala and Costa Rica (Savage, 1970), which suggests that he was not averse to land travel. Thus, it might be supposed that Warszewicz stopped along the main thoroughfare at such a place as Santiago de Veragua.

Many of the specimens collected by Warszewicz are in the Kraków and Berlin Museums. Those in the former institution bear well-defined places of origin, or ones where the place-names are qualified (e.g., Provincia de Veragua), whereas all those in the latter are limited to Veragoa (Lichtenstein, 1856:32; Savage, 1970:278). Thus, it seems safe to assume that Warszewicz kept reasonably accurate collecting notes, and that either the locality data for the Berlin material was subsequently lost, or that the specimens actually came from the environs of Santiago de Veragua. That the sea-snake *Hydrophis bicolor*

(= *Pelamis platurus*) collected by Warszewicz was said to have come from "Veragoa" (Lichtenstein, 1856:32) implies that at least a 30 km. radius is associated with this interpretation (see also Savage, 1970:279). Though it is appealing to formalize our conclusions by restricting the type-locality, especially since Santiago occurs within the geographic range of *S. lineolatus* (Fig. 16), we refrain from doing so because of the circumstantial nature of the evidence and because no other collections are available to corroborate the existence of that species in the immediate vicinity of the town. Also, the occurrence of such species as *Eleutherodactylus biporcatus*, *E. punctariolus*, *Bufo typhoni*, *Atelopus varius maculatus*, and *A. v. adspersus* (fide C. W. Myers, pers. comm.) among Warszewicz' 1851 collection with the same datum as *S. lineolatus* and *Pelamis platurus* certainly indicates that "Veragoa" pertains to a region and not to a specific locality.

SPECIMENS EXAMINED.—COLOMBIA: ANTIOQUIA: Villa Arteaga (FMNH 78132). BOLÍVAR: Cartagena, 2 m. (FMNH 165813). CHOCÓ: Curiche (FMNH 170058); Río Juradó, 200 m. (ANSP 25190); Unguía (FMNH 63818); Parque Nacional Natural Los Katíos, surrounding Alto de Limón, 800 m. (INDR 1283). SUCRE: 9 km. N Tolúviejo, 100–200 m. (ICN 3218–21).

PANAMÁ: CANAL ZONE: Alhajuela, ca. 16 km. up Río Chagres from Gamboa (CM 6861); Ancón Hill (UF 50235, 50244); Barro Colorado Is. (ANSP 24583; AMNH 47017, 63406, 89869–70; CM 7672; FMNH 13391, 13438, 56472, 178082–84; KU 75782–83, 113096–97, 172878; MCZ 25090, 28054–57, 28201, 29770; UMMZ 61612, 62638, 63742–43, 65428–29, 76003, 101795, 112332, 124890–93); Barro Colorado Is., Shannon Trail (UMMZ 63740–41); Caño Saddle (USNM 69587); Las Cascadas, cocoa plant (MCZ 19469); Corozal, Fort Clayton (UIMNH 46791–832); Is. Culebra (MCZ 18417–18); Gatún (ANSP 20857); Gatuncillo, 30 m. (AMNH 71712–15, 120146–53); Gorgas Rd., Gorgas Apts. (UMMZ 167687); Fort Clayton (UIMNH 42303); Fort Gulick (ANSP 25103); Juan Mina (UMMZ 135368a-b, 135372); Fort Kobbe (KU 116874); Madden Forest Reserve, Cruces Trail (KU 113098); Madden Lake Boy Scout Camp (UF 50239–43); Paraíso (USNM 48553); Summit Gardens (MVZ 57481; UMMZ 155800, 167685); hills nr. Venado Beach, nr. Howard AFB (KU 116873); locality unknown (FMNH 6076, 16699–700; GML [= USNM 54219]; USNM 54220). COCLÉ: Puerto Obaldía (USNM 48596). CHIRIQUÍ: Islas Secas (USNM 96032). COLÓN: Ciri-cito (CAS 71471–72); Puerto Bello (ANSP 23378; USNM 48527); Río Cascajal, Puerto Bello (USNM 54262). DARIÉN: Upper Río Subcutí (AMNH 37904); Río Chucunaque, 183 m. downstream from Río

Canglón (UMMZ 124885); 1.6 km. W El Real (UF 50234); ca. 3.2 km. S Santa Fé (FMNH 170123); Yaviza (AMNH 102548–49). LOS SANTOS: Los Santos, 16 m. (KU 113025–26). PANAMÁ: Río Bayano (FMNH 16763); GML Field Station on Río Bayano, lat. 9°09'N, long. 78°52'W, 250 m. (UMMZ 135351); Cabima, ca. lat. 9°08'N, long. 79°34'W (USNM 48502); cliffs W Cerro Campana (FMNH 60120); 6.1 km. W Chepo (UMMZ 128821); 8 km. NNW Chepo, Madroño (UF 50237); La Chorrera (FMNH 68155); Las Cumbres (UF 50236, 50238); La Joya, 15 m. (AMNH 71710); Río Mamoní (FMNH 16698); Panamá City (GML unnumbered; UMMZ 147679); Is. Saboga (MCZ 10934–37, 10939–42, 10944); San Francisco, nr. Panamá City (GML); Is. San Miguel (CAS 39515–16); Río Silugantí [= Chulugantí] (UMMZ 124888–89); Is. Taboga (CAS 98402; UF 24962; USNM 48513–16). VERAGUAS: Bahía Honda, N Punta Jabalí (CAS-SU 7461). SAN BLAS: Sasardí Camp (FMNH 170051, 170054, 212528). PROVINCE UNKNOWN: (BMNH 98.4.28.168; FMNH 212528; UMMZ 48077). “Veragoa” (ZMB 417, 36279b–c).

Sphaerodactylus millepunctatus Hallowell

Figs. 6–9, 16, 18

- Sphaerodactylus millepunctatus* Hallowell (1861:480). Type-locality: Nicaragua [herein restricted]. Syntypes: USNM 6057a–b (lost). Collector: Charles Wright.
- Sphaerodactylus millepunctatus*—Cope (1862a:499), Taylor (1956b:49), Smith and Terentjev (1963:367), Troschel (1865:599), Peters and Donoso-Barros (1970:253), Schwartz (1973:142.2), Savage (1980:77), Villa (1983:28).
- Sphaerodactylus glaucus*—Cope (1874:68; 1875:118).
- Sphaerodactylus glaucus* (part)—Günther (1885–1902:82), Barbour (1921:240), Schmidt (1941:489).
- Sphaerodactylus lineolatus*—Müller (1890:289), Noble and Klingel (1932:14), Dunn and Emlen (1932:26), Stuart (1934:9; 1935:283; 1937:68; 1948:46; 1950:52; 1958:12, 20), Schmidt (1936:47), Gage, Hartweg, and Stuart (1937:8), Malkin (1956:169, 177–178; 1958:87), Taylor (1956a:283), Taylor (1956b:40), Duellman (1963:232), J. Peters (1964:83; 1967:34), McCoy (1966:306).
- Sphaerodactylus lineolatus* (part)—Günther (1885–1902:82), Cope (1887:27), Dunn (1940:189), Smith and Taylor (1950b:52), Stuart (1963:56), Peters and Donoso-Barros (1970:252), Lee (1980:57), Mechler (1968:355), Villa (1983:28).
- Sphaerodactylus lineolatus* Var. B.—Boulenger (1885:222).

- Sphaerodactylus argus continentalis* Werner (1896:345). Type-locality: Honduras. Holotype: Petersburger Museums [ZIN 8880 (Smith and Terentjev, 1963)]. Collector: A. Schlüter.
- Sphaerodactylus argus continentalis*—Schmidt (1936:47), Smith and Alvarez del Toro (1962:103), Smith and Terentjev (1963:367).
- Sphaerodactylus argus*—Meerwarth (1901:18).
- Sphaerodactylus continentalis*—Smith and Alvarez del Toro (1962:102), Wermuth (1965:165), Smith and Taylor (1966:18), Peters and Donoso-Barros (1970:253), Hahn (1971:111), Alvarez del Toro (1973:43, 166; 1982:66, 220), Meyer and Wilson (1973:12), Wilson and Hahn (1973:105), Schwartz (1973:142.2), Thomas (1975:192), Smith and Smith (1976:L-G-6), Villa (1983:28).
- Sphaerodactylus continentalis* (part)—Savage (1973a:10).
- Sphaerodactylus* sp.—Müller (1878:573, 708), Alvarez del Toro (1973:43, 166; 1982:68, 220).

NEOTYPE: UMMZ 173053, an adult male collected by Jaime Villa (JV 68049), 10–20 January 1968.

TYPE LOCALITY (restricted by neotype selection): NICARAGUA: RÍO SAN JUAN; Isla Mancarrón of the Solentiname Archipiélago, 11°10'N, 85°02'W.

DIAGNOSIS.—A moderately large sphaerodactyl, adult size 23.6–30.5 mm. SVL. Dorsal trunk scales essentially homogeneous, keeled, 47–74 axilla-groin. Ventrals 27–37, averaging 52.4% of dorsal count. Scales around midbody 60–86. Parietal scales usually keeled. Two supranasals, anterior pair separated by one or, infrequently, two internasals (Fig. 6). Rostral with long median cleft and small posterior notch intruded by part of a small scale. Fourth supralabial lies below anterior half of eye; fourth infralabial below center of eye. Subcaudal scales enlarged, may be widened, 3–4 times width of supracaudals; aligned in a median series (Fig. 7). Escutcheon bell-shaped, composed of 22–138 total scales, usually with subfemoral extensions; 8–29 scales wide. Juvenile pattern light brown with dark bands or paired crescents ahead of and/or over forelimb and a suprapelvic spot (Fig. 8A). Distinctive markings fade in adults which develop a secondary pattern of minute dark or dark and light spots (Fig. 8B). Longitudinal lines on head become reticulate in male.

Sphaerodactylus dunni, *S. homolepis*, and *S. lineolatus* lack the median subcaudal scale series of *S. millepunctatus*. *Sphaerodactylus graptolaemus*, *S. homolepis*, and *S. lineolatus* have one supranasal, not two. *Sphaerodactylus glaucus* may be distinguished from *S. millepunctatus* by its smooth dorsal scales. There are never fine, alternating, black and white longitudinal lines over the entire dorsal surface (young) nor longitudinal series of ocelli (adult) in *S. millepunctatus*, as there are in *S. argus*.

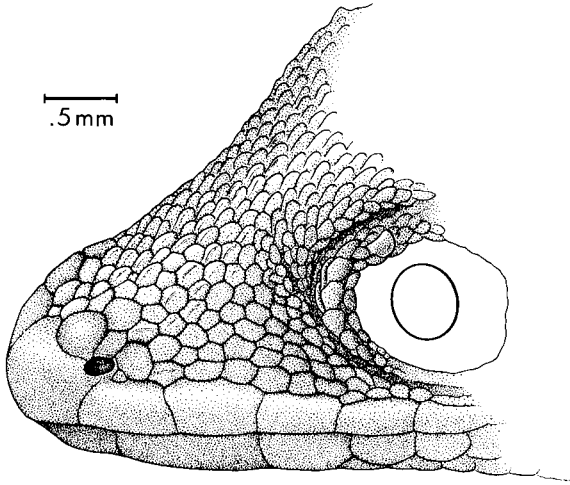


FIG. 6. Head squamation of *Sphaerodactylus millepunctatus* (UMMZ 173053).

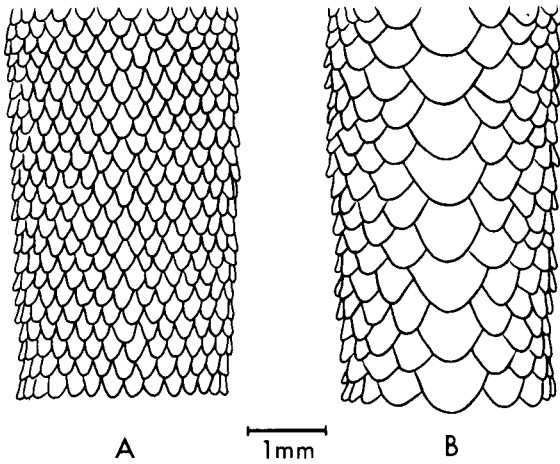


FIG. 7. Supracaudal (A) and subcaudal (B) squamation of *Sphaerodactylus millepunctatus* (UMMZ 173053).



FIG. 8. Color-patterns of *Sphaerodactylus millepunctatus*. A. Juvenile (LACM 47790). B. Adult male (ZIN 8880). Drawn by D. M. Harris.

DESCRIPTION OF NEOTYPE.—(Differing information for holotype of *Sphaerodactylus argus continentalis*, also a male, appears in parentheses). A modest-sized sphaerodactyl, 25.7 (29.6) mm. SVL. Snout-ear distance 6.1 (6.7). Head width 4.2 (4.7). Head depth 2.8 (2.7). Snout short, its length equal to distance from ear to posterior third of eye. Sides of snout converge at a 49° (50°) angle; tip blunt. Tail 27.1 mm., including a 3.5 mm. regrown tip (31.0, complete).

Rostral with long median cleft and short posterior notch occupied by single small scale. Supranasals two, anteriormost larger, rounded, dorsally confined, in narrow contact with nostril, separated from first supralabial by posterior supranasal and two small postnasals behind nostril and by rostral ahead of nostril. Internasals two (one), occupying space as wide as (less than) breadth of supranasal. Snout scales swollen, keeled, juxtaposed, 12 (nine) from orbits to rostral, four per IOW; scales narrow between eyes. Parietal surfaces and nape covered with swollen keeled granules; about five per IOW. Ocular spine short.

A short fifth supralabial and the fourth infralabial lie below eye. First infralabial largest, its length equals 1.33 IOW. Mental large, as long as wide, with oblique infralabial borders. Postmentals polygonal, not elongated; two border mental. Gular scales smooth, granular, five per IOW.

Dorsal scales of trunk oval, flattened, keeled, imbricate; about four per IOW; 51 (62) axilla-groin. Lateral scales similar to dorsals. Ventrals two per IOW; 34 (35) axilla-groin. Ventral count 67% (56.5%) of dorsal count. Scale rows around midbody 73 (72). Escutcheon bell-shaped with subfemoral extensions, about 92 (66) total scales, nine scales long by 24 rows wide (eight by 15). Supracaudal scales rhomboid, flat, imbricate, keeled at tail base as far as hindlimb extends, smooth distally; two per IOW. Subcaudal scales smooth, larger than supracaudals; scales of median series largest, slightly widened, four times width of a supracaudal scale. Pair of distinctly swollen granules at each corner of vent. Limb squamation corresponds to that of trunk. Digit scales smooth, imbricate, transversely expanded into lamellae below; 10 (11) under fourth toe.

The somewhat faded neotype still shows a pattern of small dark spots on the dorsum, each one being 1–4 scales large. Spotting grades into reticulation on the neck and head, also somewhat reticulated on tail. Preaxillary marks and light centered suprapelvic spot barely distinguishable. Underside lighter, peppered with melanophores, most intensely on chin and throat. Except for light spot on knee and bands on toes, limbs patterned like trunk. The holotype of *S. a. continentalis* is figured (Fig. 8B).

VARIATION.—A large series of *S. millepunctatus* was available from Coyoles, Honduras ($N = 58$). In this series, males tended to be smaller than females, measuring 23.6–30.4 ($\bar{x} = 26.3$, $s = 1.19$, $N = 32$) and 24.1–30.5 ($\bar{x} = 27.9$, $s = 1.90$, $N = 24$) mm. SVL, respectively. AMNH 75441 from Bonanza, Zelaya, Nicaragua was the smallest individual (12.2 mm. SVL). Snout-ear distance 20.6–24.5% of SVL ($\bar{x} = 23.2$, $s = 0.79$, $N = 20$). Head width 60.6–78.2% of head length ($\bar{x} = 66.9$, $s = 3.79$, $N = 20$). Head depth 39.1–50.9% of head length ($\bar{x} = 44.5$, $s = 3.18$, $N = 20$). Sides of snout converge at a 41–51° angle ($\bar{x} = 46$, $s = 2.5$, $N = 20$); tip rounded. Original tail 94.0–98.4% of SVL ($\bar{x} = 96.0$, $s = 1.75$, $N = 7$, including three from Coyoles). One internasal in about 85% of specimens, two otherwise. Snout scales 8–11 (mode = 9). Elongate fourth supralabial usually below anterior half of eye. Dorsals 47–74 ($\bar{x} = 58.8$, $s = 5.04$, $N = 57$); ventrals 27–37 ($\bar{x} = 30.8$, $s = 2.15$, $N = 56$), 44.3–63.6% of dorsal count ($\bar{x} = 52.6$, $s = 4.41$, $N = 56$). Scales around midbody 60–80 ($\bar{x} = 69.6$, $s = 3.58$,

N = 55). Escutcheon composed of 59–138 total scales (\bar{x} = 101.2, s = 17.37, N = 19); 6–13 by 12–31. About 22 scales between the knees; detectable escutcheon scales may or may not reach knee level. Males have two (1–3) greatly swollen granules just behind corner of vent. Infradigital lamellae of fourth toe 9–13 (mode = 11).

The Coyoles sample is about as varied in pattern as the species is throughout its range. The primary markings include dark rings at the tip of the tail, a dark suprapelvic spot and markings on the body near the forelimbs. These latter marks may appear as crescents, crosses, or bands (Fig. 8A). The primary marks fade and may completely disappear in the adults, being replaced by dark speckling (Fig. 8B). The lines and spots on the head, neck, and throat become thickened in adult males. Most males in the sample had a dorsum with light to moderately dense spotting, 1–2 scales involved per spot, and the top of head with dark longitudinal lines (occasionally reticular) breaking into reticulation on neck. The throat is lined or spotted, and a dark bar extends along posterior thigh. The limbs exhibit three large light spots.

There were notable color pattern differences in three local samples, two insular and another near the western extreme of the range. Specimens from Isla Cozumel lack the large primary markings. They are speckled with light and dark points. On top of the tail, the light spots, surrounded by black, are organized in dorsolateral pairs. Isla Roatán specimens have indefinite dark speckling, and dorsolateral yellow lines pass over the pelvic area and curl inward shortly past the base of the tail. Specimens from Estación Juárez, Chiapas may develop a pattern of large, jagged spots.

Among the characters which we have used to diagnose the species, single supranasals were found in only three *S. millepunctatus* specimens, and they were single on both sides in only one (MCZ 13453). The median subcaudal scale row was interrupted in only two specimens. Keels on the dorsal scales were imperceptible in two small specimens.

Escutcheon size and form are highly variable in *S. millepunctatus*. The structure is always bell-shaped, extending only to the groin in some specimens, but to the knee in others. Most specimens from Belize, Guatemala, and continental México have very few or no glandular scales beneath the thighs; most from Isla Cozumel, Costa Rica, Honduras, and Nicaragua have several subfemoral glandular scales. In the Coyoles, Honduras, sample, escutcheon width was not significantly related to SVL, unlike *S. homolepis*, *S. glaucus*, and *S. lineolatus* (SVL by total count).

Mexican specimens of *S. millepunctatus* were found to have substantially higher dorsal scale counts than those from Costa Rica. The dorsal count, when plotted along a transect, from 16°N 90°W to 12°N 86°W, is clearly clinal (Fig. 9).

DISTRIBUTION.—Northern Costa Rica to the Isthmus of Tehuantepec, México, excluding the northern Yucatán Peninsula. Also known from Cozumel, Roatán, Guanaja, and Maíz Grande islands.

REMARKS.—The lost syntypes came from southern Nicaragua. Their collector, Charles Wright, a botanist, is known to have become detached from Rodgers' North Pacific Exploring Expedition in San Francisco in October, 1855, from where he ". . . came home by way of San Juan del Sur and Nicaragua, botanizing for a few weeks upon an island in the Lake, and thence by way of Greytown (= San Juan del Norte) to New York" (Gray, 1886). From correspondence to Asa Gray, Wright is known to have been in Nicaragua from 20 February to 16 April, 1856 (Elizabeth Shaw, pers. comm.). The neotype comes from the region in which Charles Wright is known to have collected.

The two syntypes of *S. millepunctatus* could not be found at the USNM, nor among unidentified specimens from Cope's estate (at ANSP and USNM) by D. M. Harris. Jay Savage (pers. comm.) suggested that the missing types were probably destroyed in the Academy (ANSP) fire of 1871, because other Rodgers' Expedition types are also missing, except those which were not on loan to Cope at the time.

Hallowell's original description of *S. millepunctatus* was brief:

Spec. char. Dorsal scales very small, uncarinate; color reddish, with numerous small brownish spots; under parts white; length of head and body, 11 lines [= 23.3 mm].

Description. Scales upon muzzle larger than those upon the vertex; those upon body remarkable for their small size, being much smaller than those of the specimens in the Museum, marked *nigropunctatus*, from Jamaica, or of *Sphaerodactylus fantasticus*, from Mexico. Abdominal scales carinated, very much larger than those upon the throat and chin; color reddish-brown above, with numerous brown spots, intermingled with very minute white points; under parts white. Two specimens.

The geographic specification "Nicaragua" that appears in the paper's heading and the color description are the only two factors which allow the name *S. millepunctatus* to be related to a particular set of *Sphaerodactylus* populations. All other parts of the original description are consistent with our concept of *S. millepunctatus*, except for keeled abdominal scales. Cope (1862a:499) redescribed *S. millepunctatus*, and the information that he gave concerning pattern ("A transverse crural

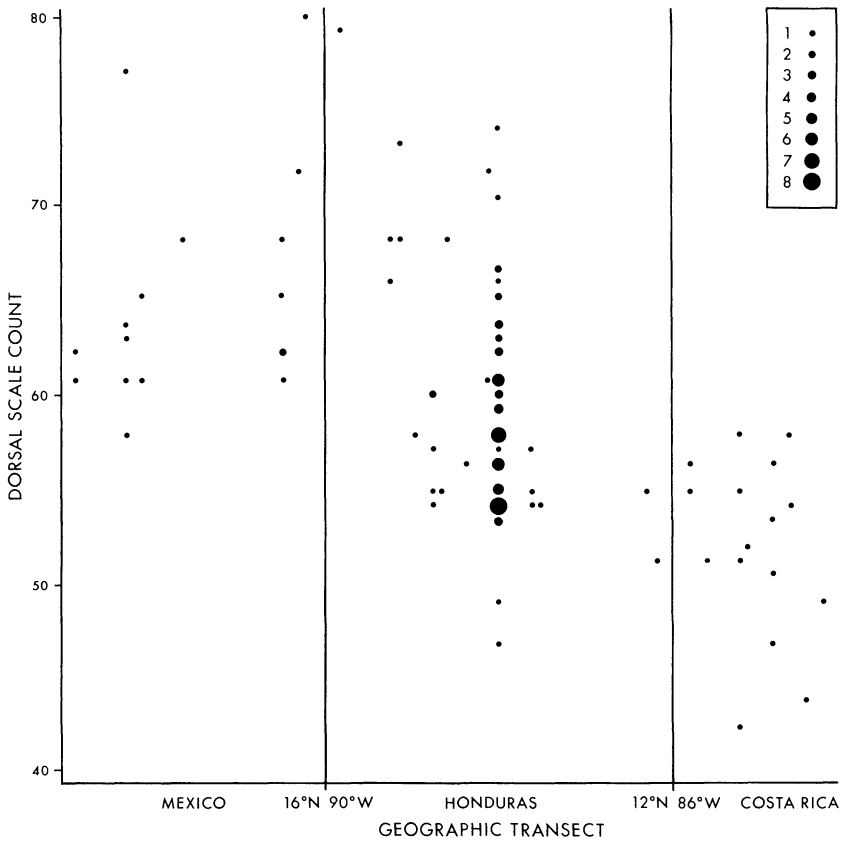


FIG. 9. Clinal variation in the axilla-groin dorsal scale counts of continental specimens of *Sphaerodactylus millepunctatus*. Dot size denotes number of coincident specimens.

spot, brown bordered posteriorly with white”) and ventral scale form (“Dr. Hallowell’s statement that the ventral scales are keeled, appears to be incorrect”) leaves little doubt as to the application of the name.

Cope (1865) later described *S. glaucus* and still later appears to have confused the two taxa. He indicated that *S. glaucus* had come from Sipurio, Costa Rica (Cope, 1875:118) and from Bransford’s Nicaraguan collections (Cope, 1874:68, probably in reference to the specimens ANSP 7563–65 from Machuca which have been missing since 1952).

The name “*continentalis*” has received much attention. Most importantly, Smith and Terentjev (1963) requested that it be placed on the *Official List of Specific Names in Zoology*, and that the application of

the name be limited to the *S. lineolatus* of Taylor (1956b:40; = *S. millepunctatus* of Taylor, 1956b:49). Both requests were refused (International Commission on Zoological Nomenclature, 1979), in part, because the proposed holotype, ZIN 8880, was mislabeled and claimed by Smith and Terentjev to lack important diagnostic characters, leaving the taxon *Sphaerodactylus argus continentalis* Werner a *nomen dubium*. Though the origin, date, and collector's name on a label attached to the specimen were consistent with the published information, the specimen was found under a different name and it was not labeled as a holotype. Through the courtesy of Ilya S. Darevsky, we examined ZIN 8880 and its characteristics are summarized with the neotype description above. On the basis of the redescription plus the supporting collection data, we conclude that ZIN 8880 is the holotype of *S. argus continentalis* Werner, that the taxon is not a *nomen dubium*, and that it is a junior synonym of *S. millepunctatus*.

SPECIMENS EXAMINED.—BELIZE: BELIZE: Manatee (FMNH 4261). STANN CREEK: Cockscomb Mts., E slope (CM 8484). PROVINCE UNKNOWN: (MPM 8242).

COSTA RICA: ALAJUELA: 1.6 km. W La Fortuna (KU 125521); 1.6 km. NE Muelle del Arenal, 70 m. (CRE 2643). GUANACASTE: Hacienda Los Inocentes (UCR 6107–9); Las Cañas, Tenorio (KU 40501–5); 4 km. E Tilarán (KU 36123); 5 km. SE Tilarán (UCR 3167). HEREDIA: Puerto Viejo de Sarapiquí (UMMZ 173047–48); Pulpería Puerto Viejo, Puerto Viejo (UCR 6622).

GUATEMALA: ALTA VERAPAZ: Panzos (UMMZ 91148); Cacao, Trece Aguas (USNM 38136). EL PETÉN: 1.6 km. W Ceibal ruins (KU 157141); 15 km. NW Chinajá, 120 m. (KU 59788); Piedras Negras (USNM 113084); Tikal (UF 13498, 13500, 13696; UMMZ 117873a–e); Toocog (= The Ohio Oil Company Of Guatemala), 15 km. SE La Libertad (KU 55868); Uaxactún (MCZ 24497–500; UMMZ 70444–46). EL QUICHÉ: Chinique (CAS 143372). IZABAL: Puerto Barrios [on bananas in Philadelphia] (USNM 64911); Puerto Barrios [on bananas in New Orleans] (USNM 69866–67); Escobas, opposite Puerto Barrios (FMNH 20020); El Golfete, S shore (ANSP 22154); between Cayo Piedra and San Gil (ANSP 22155); Quiriguá (USNM 58954); 5.1 km. W Santo Tomás, 104–152 m. (KU 187011). PROVINCE UNKNOWN: on imported bananas (USNM 71154).

HONDURAS: ATLÁNTIDA: La Ceiba (USNM 55245); 10.9 km. W La Ceiba, 8 m. (TCWC 21966); Lancetilla (ANSP 25896a–d; FMNH 21832; MCZ 32200, 39711); Tela (FMNH 13183; LSUMZ 24599); Tela [on bananas in Baltimore] (USNM 64173); Tela [on bananas in New Orleans] (USNM 69863, 70460–61). ISLAS DE LA BAHÍA: Is.

Guanaja, 2 km. W Sabana Bight (LACM 47778); Is. Roatán (UF 28489); Is. Roatán, nr. Coxen Hole (FMNH 34541); Is. Roatán, 3.2 km. W Roatán, Coxen Hole (CM 64527); Is. Roatán, ca. 3.2 km. W French Harbor (LSUMZ 22338–40, 22390, 22392); Is. Roatán, nr. French Harbor (CM 64525); Is. Roatán, Gibson Bight (LSUMZ 33796–97); Is. Roatán, Port Royal area (MCZ 150935); Is. Roatán, Port Royal area, beach N Cow Key (TCWC 52427–28); Is. Roatán, N side opposite Port Royal (LSUMZ 33806–8); Is. Roatán, Port Royal Harbor, Jennings's Point (LSUMZ 33801). COLÓN: Balfate (AMNH 58621); Puerto Castilla [collected on bananas] (USNM 64932); El Dorado, nr. Barranco (UMMZ 58408); 0.5 km. S Trujillo (LACM 47809). COMAYAGUA: ca. 8 km. S La Misión (MCZ 49975); Pito Solo (CM 64526); Lago de Yojoa, 1.6 km. Pito Solo (LSUMZ 28528–29). COPÁN: El Jaral [Rancho], along Río Amarillo (LACM 45391). CORTÉS: Río Santa Ana, W San Pedro, 244 m. (FMNH 5029); Laguna Ticamaya, W San Pedro (FMNH 5032–35, 5226). OLANCHO: Catacamas (LACM 45137–39); 4.5 km. SE Catacamas (LACM 47777). YORO: Corinto, Subirana Valley (MCZ 38795); Coyoles (LACM 47783–808); 0.5 km. N Coyoles, 180 m. (LACM 47779–80; LSUMZ 21441); Coyoles, 180 m. (LSUMZ 21442–74); Los Indios [farm] (MCZ 38796); Progreso, ca. 30 m. (UMMZ 58380); San Francisco (MVZ 52401); Rancho San Lorenzo, 25 km. WSW Coyoles (LACM 47782). PROVINCE UNKNOWN: (USNM 71733, 79951, 82573–74, 86862, 95866–67, 98909; ZIN 8880).

MEXICO: CHIAPAS: Palenque (LACM 65133); Rancho Alejándria, 6 km. NE Estación Juárez (UCM 49382–86). OAXACA: Palomares, Juchitán (UCM 39789–90). QUINTANA ROO: Is. Cozumel (FMNH 153463; USNM 47644); Is. Cozumel, Punta Norte (MCZ 149565); Is. Cozumel, San Miguel (UCM 16188–90; UMMZ 78564, 84352); Is. Cozumel, 6 km. NE San Miguel (ASFS-V 7187); Is. Cozumel, 6 km. S San Miguel (ASFS-V 23492). TABASCO: mogote [= hummock], 4.2 km. E Teapa (RT 1354); mogote #1, 3.9 km. E Teapa (RT 1355).

NICARAGUA: CHONTALES: locality unknown (BMNH 94.10.1.1). MANAGUA: Casa Colorada, ca. 22 km. S Managua (UMMZ 173049–50). MATAGALPA: Hacienda La Cumplida, 732 m. (UMMZ 117591a–c). RÍO DE SAN JUAN: Archipiélago de Solentiname, Is. Mancarrón (UMMZ 173053–54). ZELAYA: Bluefields (UMMZ 173051); Bonanza, 259 m. (AMNH 75441; KU 84866); Camp Corozo, Río Wawa-Sang [Río Wawashan] (AMNH 70509); Is. Maíz Grande (UMMZ 173052); Cukra (AMNH 17132); Río Escondido (USNM 19878–81); Musawas, Río Waspuk (AMNH 75439–40); Río [=Caño] Pichinga, back of Laguna de Perlas (AMNH 70519); 11.3 km. above Rama, Río Siquía

(UMMZ 79802); 16.1 km. above Recero [= Recreo], Río Mico (UMMZ 79801); Wounta Haulover (ANSP 15841, 15843). PROVINCE UNKNOWN: (AMNH 16278-79, 16285).

UNITED STATES: MISSISSIPPI: Starkville [on bananas] (USNM 65451).

Sphaerodactylus glaucus Cope

Figs. 10-12, 17-18, Table 1

Sphaerodactylus glaucus Cope (1865:192). Type-locality: México: Yucatán; near Mérida. Holotype: USNM 6572. Collector: Comisión Científica under Arthur Schott.

Sphaerodactylus inornatus W. Peters (1873:738). Type-locality: México [dubiously restricted to Tehuantepec, Oaxaca, by Smith and Taylor (1950a:340; 1950b:53)]. Lectotype by present designation: ZMB 36187 (formerly 4589). Paralectotype: ZMB 4589. Collector: Uhde.

Sphaerodactylus torquatus Strauch (1887:35). Type-locality: Mazatlán. Syntypes: ZIN 3268a-c. Collector: Salmin.

Sphaerodactylus glaucus—Cope (1866:125; 1871:216; 1872:137), Troschel (1866:184), Bocourt (1873:46; 1876:401), Sumichrast (1880:162, 173; 1882a:277; 1882b:35), Boucard (1885:309), Boulenger (1885:221), Strauch (1887:35), Dugès (1896:479, 484), Gadow (1905:194, 211), Barbour (1921:240, 275; 1929:342), Stuart (1934:8; 1935:41; 1937:68; 1948:46; 1950:22, 58; 1963:55), Gaige (1936:295), Schmidt (1936:47), Smith (1938:13), Hartweg and Oliver (1940:14), Smith (1941:43; 1946:75), Pearse (1945:217), Taylor (1947:305), Taylor (1956b:32), Grant (1959:199), Alvarez del Toro (1960:71), Barrera (1962:89), Smith and Terentjev (1963:367), Wermuth (1965:167), Peters and Donoso-Barros (1970:252), Schwartz (1973:142.2), Lee (1980:56).

Sphaerodactylus glaucus (part)—Günther (1885-1902:82), Cope (1887:27), Schmidt (1941:489).

Sphaerodactylus glaucus glaucus—Smith (1949:34; 1960:223), Smith and Taylor (1950a:352, 1950b:53), Werler and Smith (1952:553), Maldonado-Koerdell (1953:130), Smith and MacDougall (1954:21), Stuart (1954:51; 1958:12, 20), Mertens (1956:384), Taylor (1956a:283), Neill and Allen (1959:33), Smith (1960:223), Cochran (1961:146), Neill (1962:84; 1965:90), Smith and Alvarez del Toro (1962:102), Stuart (1963:55), Duellman (1965:594), Wermuth (1965:168), Lynch and Smith (1966:58), McCoy (1966:306), Thatcher (1966:92), Peters and Donoso-Barros (1970:252), Fitch (1970:21), Alvarez del Toro (1973:42, 166; 1982:66, 220), Smith and Smith (1976:L-G-6).

- Sphaerodactylus glaucus inornatus*—Smith and MacDougall (1954:22), Taylor (1956a:283; 1956b:168), Smith and Alvarez del Toro (1962:102), Smith and Taylor (1966:18), Peters and Donoso-Barros (1970:252), Smith and Smith (1976:L-G-6).
- Sphaerodactylus glaucus torquatus*—Smith (1949:35), Smith and Taylor (1950a:338; 1950b:53), Werler and Smith (1952:553, 556), Maldonado-Koerdell (1953:131), Mertens (1956:384).
- Sphaerodactylus inornatus*—Troschel (1874:161), Taylor (1947:301), Smith and Taylor (1950a:340).
- Sphaerodactylus lineolatus* (part)—Barbour (1921:238).
- Sphaerodactylus torquatus*—Günther (1885–1902:82), Gadow (1905:211), Taylor (1938:506; 1947:302; 1956a:283), Smith and MacDougall (1954:24), Duellman (1965:594), Mertens (1956:384), Smith and Alvarez del Toro (1962:102), Wermuth (1965:174), Smith and Taylor (1966:18), Schwartz (1973:142.2), Smith and Smith (1976:L-G-6).
- Sphaerodactylus glaucus* (unconfirmed)—Heinemann (1877:431), Velasco (1892:75), Allen (1928:98).
- Sphaeriodactylus* [from Vera Cruz]—Heinemann (1877:431).

DIAGNOSIS.—A medium-sized *Sphaerodactylus*, smallest specimen with recognizable escutcheon 20.0 mm. SVL, largest male 27.2 mm., largest female 29.2 mm.; females generally two mm. longer than males. Dorsal trunk scales homogeneous, smooth, 46–71 axilla-groin. Ventrals 26–37, averaging 55% of dorsal count. Scales around mid-body 53–88. Parietal scales smooth. Two supranasals, anterior pair separated by one or, infrequently, two internasals. Rostral with long median cleft and small posterior notch filled by part of a small scale. Fourth supralabial lies below anterior half of eye; fourth infralabial below center of eye. Subcaudal scales enlarged, widened, aligned in median series. Escutcheon bell-shaped, composed of 19–97 total scales, usually with subfemoral extensions; 5–9 scales long and 6–29 rows wide. Pattern highly variable.

All of the Middle American sphaerodactyls, except *S. glaucus*, have keeled dorsal scales.

REDESCRIPTION OF HOLOTYPE.—(Where differing, information for the lectotype of *S. inornatus* is included in parentheses.) Female, SVL 24.5 mm. (30.2), snout-ear distance 5.6 (6.8), head width 3.4 (4.6), head depth 2.4 (3.2), complete original tail (partly separated at base) 23.1 (11.5 base and 11.1 regrown part). Snout short, its length equals distance from ear to posterior fourth of eye. Sides of snout converge at 44° (51°); tip rounded.

Rostral small, crescentic from above, with short (moderate) median cleft and shallow posterior indentation occupied by part of small scale. Two supranasals. One internasal separates anterior supranas-

als. Internasals one-half diameter of anterior supranasals. Postnasal single (two postnasals). Snout scales slightly swollen (granular), smooth, juxtaposed, eight orbit-rostral, three (four) per IOW. Parietal surfaces and nape covered with smooth granules, maximally six (seven) per IOW. Fourth supralabial lies below anterior half of eye; fourth infralabial below center of eye. Mental large, its posterolateral borders slant forward. Postmentals polygonal, rounded, smooth, swollen, two (three) border mental. Gular scales smooth, granular, six per IOW; imbricating behind level of eye.

Dorsals oval-rhomboid, flat, moderately thin, imbricate, smooth, minimally four (five) per IOW, 53 (62) from axilla to groin. Ventrals oval, flat, thin, smooth, minimally two per IOW; 31 (35) between levels of limbs, which is 58.5% (56.4%) of dorsal count. Scale rows around midbody 65 (79). Scales of median subcaudal row enlarged, three (four) times supracaudal scale width. Supracaudals similar to trunk dorsals, two (three) per IOW. Limb squamation comparable to that of trunk except scales granular posteriorly and on dorsal tibial and ulnar surfaces. Digit scales imbricate, smooth, transversely expanded below into lamellae, of which there are 10 (14) on fourth toe. Coloration of holotype indistinct because of fading. (See Cope [1865] for color in life.)

The lectotype of *S. inornatus* has a dark nuchal mark between two smaller white spots which are feebly bounded by darker color. Each of the pair of light suprapelvic spots is bordered anteriorly by a dark brown crescent. Broad unicolor cream middorsal band; sides with fine dark stippling on pale medium brown. No pattern on head; limbs with traces of large light spots.

VARIATION.—Males differ little from females for the characteristics described above. Color in alcohol between the sexes is also similar, though males from Guatemala and Belize do not seem to retain the well-defined female pattern. On the tail base, lateral to the vent, mature males usually have 3–5 swollen granules in a small patch. The escutcheon is bell-shaped and extends to the knees, except in smaller males where subfemoral glandular development has not occurred; the positive correlation of escutcheon scale count to SVL is shown in fig. 11 and table 1.

Single supranasals were not found except in one specimen from "Port Guatulco" discussed below. The median subcaudal scale series contained alternating elements in two specimens, but alternation between single elements and pairs for the entire tail length was never observed.

The angle of convergence of the sides of the snout varied as greatly within as between local samples. Snout angles of samples of adults

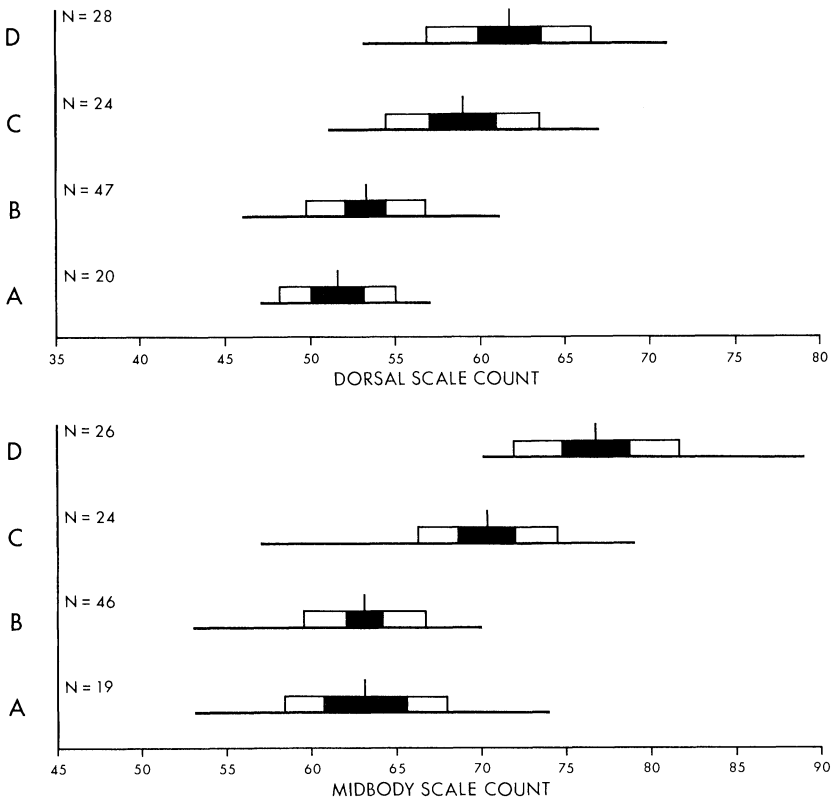


FIG. 10. Geographic variation in dorsal (axilla-groin) and midbody (circumference) scale counts of *Sphaerodactylus glaucus*. (A) Cajón de Piedra and El Limón, Oaxaca. (B) Guiengola-Tehuantepec, Oaxaca. (C) Balchacaj, Campeche. (D) Middlesex, Belize. The sample range (horizontal line), one standard deviation (open rectangle) and the standard error of the mean (closed rectangle; 95% confidence interval) are indicated around the mean (vertical line). N = sample size.

equally divided by sex from four localities (those of Fig. 10) were 42.5–53° (\bar{x} = 47.6, s = 2.74, N = 40).

Sphaerodactylus glaucus is generally a medium-sized species. The males of populations near Tehuantepec, Balchacaj (Campeche), and Middlesex (Belize) are mostly 25–26 mm. SVL, and the females are 26–29 mm. Specimens from Veracruz are larger: males to 28.2 and females to 30.8 mm. SVL.

REMARKS.—Barbour (1921:240) and Cochran (1961:146) reported a *S. glaucus* type-series of four specimens; however, some of the in-

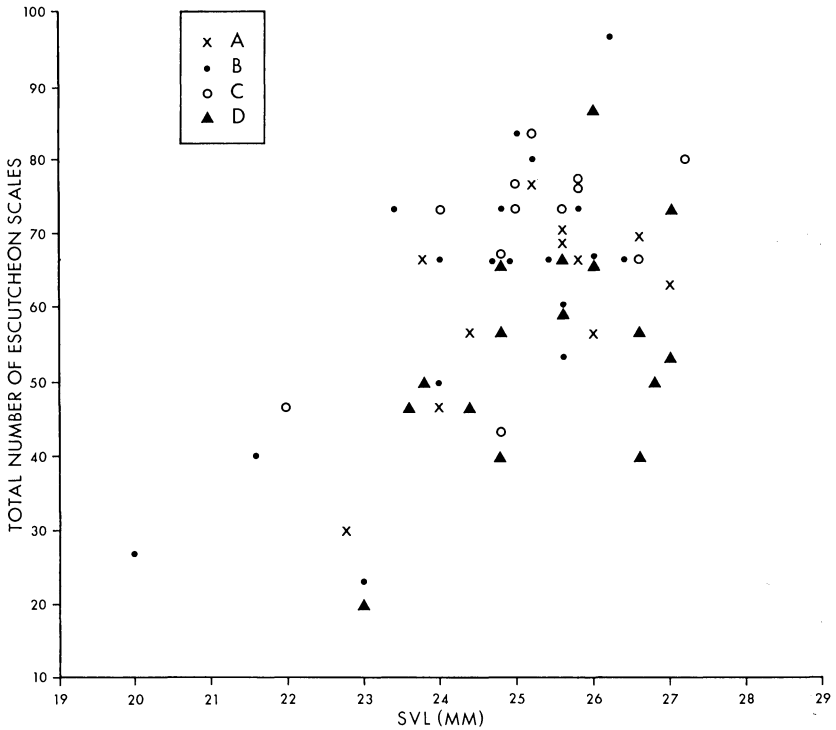


FIG. 11. Total escutcheon scales and snout-vent length in the four populations of *Sphaerodactylus glaucus* (A, B, C, and D of Fig. 10).

TABLE 1

ANCOVA OF ESCUTCHEON SCALES IN MALE *Sphaerodactylus glaucus*. SVL is the independent variate (Fig. 10). All correlation coefficients are significant ($P > 0.05$).

	A	B	C	D
N	11	18	12	17
\bar{x}	61.1	62.6	69.2	54.5
s	13.2	19.0	12.9	15.4
\bar{x}_{adj}	59.9	66.1	68.2	52.2
S.E. $_{\bar{x}}$	3.7	3.0	3.6	3.0
r	0.670	0.723	0.576	0.513

formation associated with that material leads us to believe that Cope had only one specimen. Cope's original description of *S. glaucus* was presented at the October 31, 1865 meeting of the Academy of Natural Sciences, Philadelphia and, according to the 1913 Index to the Journal and Proceedings of the Academy, the published fascicle containing his paper was first received outside of the Academy on December 21, 1865. The original catalogue entry (G. R. Zug, pers. comm.) for USNM 6572 listed two (presumably field) numbers, 837 and 973, and three specimens corrected to four specimens, all in the same handwriting, with Schott as the collector. Collection date and locality were not given as part of the initial entry. A later entry added "Progreso" Dec. 22, 1866 to 837, and "Merida" Feb. 1866 to 973. Cochran (1961:146) associated the earlier date with the specimen currently residing as USNM 6572 and the other with those recatalogued as USNM 62995–96, and MCZ 13570 (= USNM 62994). Thus, all of the "type-specimens" postdate the description. Cope's subsequent paper (Cope, 1866) containing information on Arthur Schott's Yucatán collection at the Smithsonian was presented at the May 29, 1866 Academy meetings, and in it he reported several other specimens of *S. glaucus*. These additional specimens are not presently in the USNM collection, unless they are the ones being called types, but this conclusion is not satisfactory either because of inconsistent dates. However, if there had been a transcription error, and the specimens in question were collected in 1865 instead, this would solve the problem. Cope's description of *S. glaucus* (as also noted by Barbour, 1921:240) appears to have been based on only one specimen, and USNM 6572 fits the description best. Also, Mérida, the locality given for USNM 6572, is more like the type-locality, "near Mérida," than Progreso, which is 33 km. N of Mérida. Pending a review of Schott's journals and letters, we conclude that USNM 6572 is the holotype of *S. glaucus* and that USNM 62995–96 and MCZ 13570 are not types, but rather the "several specimens" later referred to by Cope (1866:125).

Three southern Mexican sphaerodactyls are currently recognized: *S. torquatus* and *S. glaucus inornatus* from the Pacific side of the Isthmus of Tehuantepec, and *S. g. glaucus* from the Gulf side, as well as the states of Campeche, Chiapas, Quintana Roo, and Yucatán. We have examined one of the two syntypes of *S. inornatus* (ZMB 36187), and we designate it the lectotype. Contrary to the scientific name, the lectotype, though somewhat faded, shows a distinctive color pattern similar to Gulf coast specimens. It exhibits a prominent dark nuchal spot, a broad sparsely marked middorsal region, and stippled sides (as in Fig. 12E). The paralectotype (ZMB 4589), now presumed lost (G.

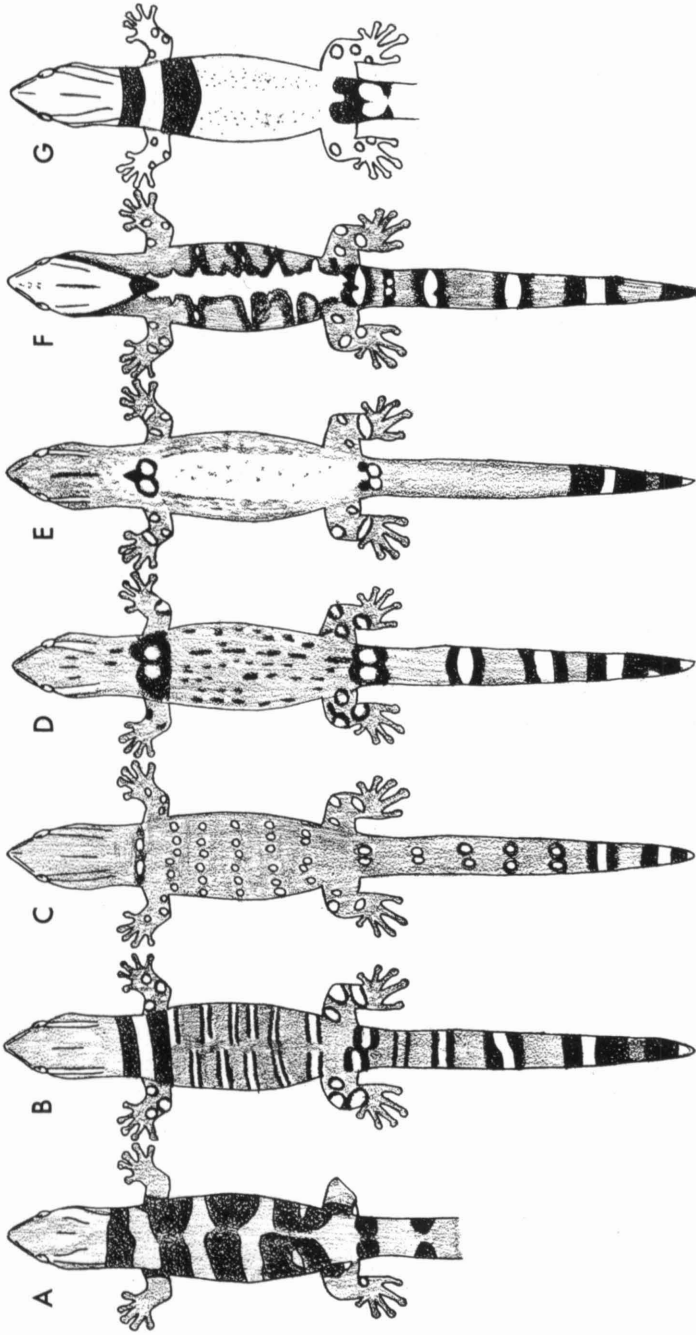


FIG. 12. Dorsal color pattern variation in *Sphaerodactylus glaucus*. (A) "Port Guatulco," south-central Oaxaca (AMNH 81487—cf. *glaucus*). (B) El Limón, Oaxaca (USNM 113136, juvenile). (C) Tehuantepec, SE Oaxaca (USNM 113146, 113154, 113161—composite juveniles). (D) Tuxtla Gutiérrez, Chiapas (UF 37460—adult female). (E) Balchacaj, Campeche (FMNH 125858—juvenile). (F) Stann Creek, Belize (UCM 45193—adult female). (G) 4 km. WSW Puerto Juárez, Quintana Roo (KU 70057—immature). Drawn by D. M. Harris.

Peters, pers. comm.), figured by Smith and MacDougall (1954:24) also has a slightly darker nuchal area and light ocelli above the vent. The dorsal (62) and midbody (79) scale counts of the lectotype are also more similar to specimens from the Caribbean side than they are to Pacific material (Fig. 10). Moreover, the lectotype is large (30.2 mm. SVL) like Gulf material from Veracruz. In general, we can find no basis for recognizing *inornatus* as a race of *S. glaucus*, and we synonymize the two names. It follows that Smith and Taylor's (1950a:340; 1950b:53) restricted type-locality for *S. inornatus*, "Tehuantepec [City], Oaxaca," is incorrect.

Smith and MacDougall (1954) regarded *S. torquatus* as a distinct species, based on the presence of a double, dark collar. They also claimed that these specimens had a pink (versus nonpink) tail, which was waved (versus not waved), and they were restricted to a terrestrial microhabitat rather than being arboreal. We have been unable to find any differences in body scalation and escutcheon counts that would corroborate the collar character (Figs. 10–11); however, *S. glaucus* from Campeche and Belize are quite different from southern Tehuantepec sphaerodactyls. Moreover, there exists considerably more variation in the collar character than Smith and MacDougall (1954) realized. Individuals with dark neck rings appear among normally nonringed local samples and vice versa. The dorsal pattern of juveniles also has two phases, spotted (Fig. 12C) and banded (Fig. 12B), which vary over the same geographic region as does the neck ring, as well as independently of the neck ring. The adult pattern also seems to have two phases: fine, and coarse dark spotting, with the former seemingly more common in collared individuals. Spearman rank correlation analyses of predominantly banded populations from Cajón de Piedra and El Limón, and the unbanded form from Tehuantepec-Guiengola Mt., show no significant relationship between neck pattern and dorsal pattern. Some of the Cajón de Piedra specimens lack dark collar bands, but still have a definite light ring where the dark bands would have been, but bordered by ground color. Using the light ring character still gives insignificant correlations.

The dark collar bands vary considerably, as acknowledged by Smith and MacDougall (1954). In hatchlings, both bands are wide (about 10 scales) and continuous, though they never cross the throat. In larger specimens the bands at their widest may be three to ten scales across and at their narrowest 0–6 scales across, and even entirely absent. Another population in Quintana Roo has collared individuals too (Fig. 12G; see also Duellman [1965:594]). Since the dark collar band

(see Smith and MacDougall, 1954:26) and both the adult and juvenile dorsal patterns occur infrequently over a wide area in the southern Tehuantepec region, we conclude that only a single polychromatic, smooth-scaled sphaerodactyl exists in southern México.

Smith and MacDougall (1954:22) claimed that the subspecies *S. g. inornatus* lacked any pink on the tail in life, the tail being gray. Inferring "pink" to mean any red tones, this is contradicted by Sumichrast's (1882a:277) detailed color-in-life description of a southern Tehuantepec example (translated): "Top of head ordinarily gray-brown; head behind eyes and neck with light stripes; dorsum vermiculated and spotted with black; above sacrum reddish-white spots with black borders, occasionally united; above, tail with three pallid red half-rings with black borders; below tail is red-orange. Lower part of limbs with light annuliform spots; chin and throat finely spotted with black; iris light brown." Again there is no corroboration for two *Sphaerodactylus* species in southern Tehuantepec as concluded by Smith and MacDougall (1954). Because the morphological and chromatic evidence for two species is either weak or nonexistent we prefer to ignore the apparently casual observations on habitat and tail waving behavior, also emphasized by Smith and MacDougall (1954), and recognize only one sphaerodactyl, *S. glaucus*.

If one were to continue to use the name *torquatus*, it could be diagnosed as lacking a dark nuchal spot and by having a uniformly marked dorsum rather than a broad, light, sparsely marked mid-dorsal zone. As such, it would be confined to the Pacific versant of the Isthmus of Tehuantepec, and might be considered a subspecies of *S. glaucus*.

Some of the high degree of color-pattern diversity of *S. glaucus* is shown in fig. 12. Specimens are plentiful from three regions, the southern part of the Isthmus of Tehuantepec, northern Tehuantepec extending into Veracruz and northwestern Yucatán, and Guatemala and Belize. In each of these regions the pattern is distinctive. Specimens from the border of the Gulf of México show a broad, pale dorsal zone, lightly stippled sides, a dark nuchal spot and a few other marks as illustrated in fig. 12E. The lighter middorsal area is faint and was not noted by Taylor (1947), Werler and Smith (1952), McCoy (1966), or Gage (1936). Southern Tehuantepec specimens (Fig. 12B–C) show narrow bands of light spots and sometimes neck rings. Also, the light limb spots tend to become obscure with age. *Sphaerodactylus glaucus* from Belize and Guatemala appear to have a combination of these patterns, namely, a light middorsal area, dark nuchal spot and light series of spots or stripes which cross the dorsum (Fig. 12F). Specimens

are rare from the three other regions, but the patterns appear equally distinctive. In Quintana Roo, there is a collared form (Fig. 12G; see also Duellman, 1965:594). In Chiapas there is a form with relatively bold markings (Fig. 12D), which is like specimens from extreme southeastern Oaxaca, except that the latter have a suprapelvic spot, as in *S. millepunctatus*. Lastly, there is a single specimen from "Port Guatulco," Oaxaca (AMNH 81487) whose color-pattern is markedly different from all other *S. glaucus*. It possesses a band across the nape and essentially three broad black bands across the dorsum. This pattern seems to be most similar to examples from El Limón (Fig. 12B); the collar band is much the same, and the light centers in the posterior body bands of the Guatulco specimen may indicate that the narrow dorsal bands (Fig. 12B) have been eliminated by the increasing spread of melanin. However, where *S. glaucus* typically has two supranasals, the Guatulco specimen has only one on each side. The specimen is a female, lacking the escutcheon, and is missing most of the tail. Only additional material exhibiting the exceptional color pattern and scalation would give force to the argument that a second smooth-scaled sphaerodactyl species occurs in southern México.

SPECIMENS EXAMINED.—BELIZE: BELIZE: Altun Ha ruins (KU 171411); Lemonal (MPM 7503); Manatee (FMNH 5827). CAYO: Xuantunich (MCZ 65377). ORANGE WALK: Albion Is. (USNM 167761); Gallon Jug (MCZ 71361); Otro Benque, 3.2 km. N Orange Walk (USNM 194119–20, 194949); Tower Hill (MPM 8279); Yo Creek (MPM 7611). STANN CREEK: All Pines (CM 8493); Citrus Research Stn., 14.5 km. W Stann Creek (MPM 7504); Melinda (MPM 13890); Middlesex (UCM 45113–93); Silkgrass (FMNH 49121); Stann Creek (BMNH 91.3.4.1, 3). TOLEDO: Pueblo Viejo (MPM 13891). PROVINCE UNKNOWN: (FMNH 4177; MPM 7561).

GUATEMALA: ALTA VERAPAZ: Cacao, Trece Aguas (MCZ 13453; USNM 38135). EL PETÉN: Altar de Los Sacrificios (AMNH 99901); Chiquimula, Esquipulas (UMMZ 106864–66); Estación Exptl. Forestal El Rosario, 4.5 km. (by rd) E Sayaxché (MVZ 149090–93); Flores (UMMZ 79084, 79085a–b); La Libertad (UMMZ 75182, 75184, 75464); 8.0–11.3 km. S La Libertad (UMMZ 75183); Piedras Negras (USNM 113085); Pueblo Nuevo, S Flores (UMMZ 79083); Sayaxché (UCM 22196); Tikal (MVZ 149094; UF 13499, 13695, 13697–700; UIMNH 52527; UMMZ 117874); Uaxactún (UMMZ 70447, 70449–50). EL QUICHÉ: Chinique (CAS 143371). IZABAL: Cayo Piedra (ANSP 22156); Las Dantas, 2.7 km. W El Estor, 29 m. (MVZ 160508; UTACV-R 8862); Santo Tomás (KU 187010).

HONDURAS: COPÁN: Copán (AMNH 124037).

MEXICO: CAMPECHE: Apazote (USNM 47796); Is. Aguada (UF 33541); Balchacaj, mouth Río Champán (FMNH 113487–504, 113506–9, 113511–17, 113519–22, 113524–34, 113537–39, 191033; UIMNH 19667–83; UMMZ 81926a–e); Ruinas Becán (KU 171412); Ciudad del Carmen (UCM 20543–44; UIMNH 19684–86); 9.7 km. NNE Ciudad del Carmen (UIMNH 86922); Chuina, 46 km. S Champotón (KU 74847); Los Coyoc, S Is. Aguada, across Laguna de Términos (UF 33540); Tuxpeña Camp (UMMZ 73233). CHIAPAS: 11.6 km. N Arriaga (UTEP 8233); Puebla Palenque (EAL 2898; UF 33543); Pichucalco (UF 33542); Tuxtla (UF 39460). OAXACA: Cajón de Piedra, 24 km. W Salina Cruz (AMNH 66947, 125265–83; USNM 113123–25, 113127–33); Cerro Arenal, nr. Tenango (AMNH 68119, 125286); nr. Chivela, 183–213 m. (MCZ 25022–26); Cosolapa (CAS 74384); El Limón (UCM 39791–95; USNM 113134–38); El Tanque, 22 km. W Tehuantepec (CAS-SU 16184–85; UIMNH 20600–602, 20604–5); Guie-Shaya, 610 m., Cerro de Mixtequilla (UIMNH 33187); vic. Huilotepec (UMMZ 82292); Is. Natardac, Laguna Superior (AMNH 68882); Juchitán (USNM 30235–38); Las Minas, ca. 8.4 km. E Tapanatepec (UTEP 8192); Las Pilas (AMNH 66945, 125263–64); Mixtequilla (AMNH 15975, 125291; CAS 73564–65; MCZ 38658); Oscuranos, slopes Cerro San Pedro, nr. Tehuantepec (AMNH 66889, 68120, 125285); Guiengola Mt., 8 km. NW Tehuantepec (AMNH 19345, 66946; UMMZ 82293–94; USNM 113121–22); between Guiengola Mt. and Tehuantepec (UMMZ 82295a–c, 82296a–b, 82297a–g, 82298a–j, 82299a–p); “Port Guatulco” [nr. Santa María Huatulco?] (AMNH 81487,—S. cf. *glaucus*); Río Hondo (UIMNH 33178); Río Los Milagros, Santa María Chimalapa (AMNH 64962); Salazar (AMNH 66943–44, 125259–62); Salina Cruz (BMNH 1903.9.30.7); W of Salina Cruz (AMNH 15976); San Antonio (UIMNH 33188); Santa María (CAS-SU 16186, 23126; UIMNH 33681–84); Santo Domingo Petapa (UIMNH 33685); Tapanatepec (MCZ 27876–77); 8.3 km. E Tapanatepec, ca. 11 km. W Oaxaca-Chiapas border, via Hwy. 190 (UTEP 7684); 8.5 km. E Tapanatepec (UTEP 8229); Tehuantepec (AMNH 58032, 64965–67, 65798–800, 77103, 125287–90; FMNH 125721–39, 179231; USNM 113139–61, 113163); 4 km. E Tehuantepec, via Hwy. 190, 30 m. (MVZ 78242–43); 4.8 km. E Tehuantepec, via Hwy. 190, 30 m. (MVZ 78244); 6.4 km. E Tehuantepec, via Hwy. 190 (MVZ 78789); 12.7 km. W Tehuantepec, 91 m. (UMMZ 115100); 4.8 km. NE Tehuantepec (UMMZ 82300a–b, 82302a–d); Finca Santa Teresa, 2 km. NW Tehuantepec (UMMZ 82303a–b); nr. Tehuantepec (FMNH 106420, 111495–500, 111502–3, 111505–6; UIMNH 19691–700); vic.

Tehuantepec (AMNH 68121–22, 125284; UMMZ 82301a–e); Tehuantepec, Cerro San Pedro (AMNH 65801); 27.7 km. NW, 3 km. NE Tehuantepec, 198 m. (UF 33544); Tuxtepec (TCWC 58008). QUINTANA ROO: Laguna de Bacalar (LSUMZ 34775–76); Chetumal (USNM 194952); 4 km. WSW Puerto Juárez, 5 m. (KU 70057); 35 km. WSW Puerto Juárez (LSUMZ 28266); locality unknown (AMNH 15950). TABASCO: Álvaro Obregón (AMNH 63629; CAS-SU 16182–83; FMNH 19001–2, 125858–83, 125154; USNM 113096–120); Balancán, Río Usumacinta (MCZ 46200); ruins 4 km. NE Comalcalco (AMNH 77059); Emiliano Zapata (EAL 3330; USNM 113095); Frontera (USNM 37749–51, 46694); Teapa (BMNH 89.11.13.19–22; UMMZ 119787a–g); 24.1 km. N Teapa (LSUMZ 6880); Tenosique (USNM 113087–94); Villahermosa (USNM 192543a–d); Villahermosa, Museo La Venta (AMNH 114842); 24.9 km. NE and 10 km. S Villahermosa (TCWC 21857). VERACRUZ: Río Coatzacoalcos (LACM 93883; USNM 61184–85); Pérez (FMNH 6415); San Andrés Tuxtla (TCWC 19125, 35062–63, 36834–35; UMMZ 121309, 121310a–c, 121311–13, 121174–76); vic. San Andrés Tuxtla Mts. (TCWC 42478–79, 51274–75); San Andrés Tuxtla, ca. 366 m. (TCWC 19627, 21349); between San Andrés Tuxtla and Volcán San Martín (UTACV-R 3190); Tezonapa (USNM 113086); Tlacoatlpan (USNM 46644–45, 46657); Tuxpan (USNM 25215); Veracruz, S end city (UMMZ 122058); locality unknown (FMNH 113510). YUCATÁN: Calcehtok (AMNH 38948); Dzibichaltún (FMNH 53460); Mérida (CM 44462; FMNH 153437; USNM 6572); Progreso (FMNH 113518, 113523, 113535–36, 113540; MCZ 13570; USNM 62995–96); 25.9 km. NE Sisal (KU 157142–46); Telchac (KU 157147); locality unknown (FMNH 191190). PROVINCE UNKNOWN: (ZMB 36187). UNITED STATES: LOUISIANA: New Orleans [?] (USNM 81166). NO DATA: (ANSP 13415; FMNH 113510).

Sphaerodactylus homolepis Cope
Figs. 1C–D, 4, 5, 13, 17–18

- Sphaerodactylus homolepis* Cope (1886:277). Type-locality: Nicaragua [restricted to between El Castillo and San Juan del Norte, along the Río San Juan and its tributaries; see Savage, 1973b]. Holotype: USNM 14207. Collector: J. F. Bransford.
- Sphaerodactylus homolepis carinatus* Andersson (1916:5). Type-locality: Costa Rica. Holotype: GNM 1325. Collector: Carl Bovallius.

- Sphaerodactylus lineolatus imbricatus* Andersson (1916:5). Type-locality: Costa Rica. Syntypes: GNM 1326a–c. Collector: Carl Bovallius.
- Sphaerodactylus mertensi* Wermuth (1965:170). Substitute name for *S. lineolatus imbricatus* Andersson, preoccupied by *S. imbricatus* Fischer, 1881.
- Sphaerodactylus mertensi*—Peters and Donoso-Barros (1970:251, 252), Schwartz (1973:142.2), Villa (1983:28).
- Sphaerodactylus glaucus*—Savage (1970:284).
- Sphaerodactylus glaucus* (part)—Cope (1887:27).
- Sphaerodactylus homolepis*—Günther (1885–1902:82), Cope (1887:27), Taylor (1956b:38), Cochran (1961:147), Smith and Terentjev (1963:367), Schwartz (1973:142.2), Savage (1973b:37; 1980:77), Villa (1983:28).
- Sphaerodactylus imbricatus*—Taylor (1956b:45), Grant (1959:199), Smith and Terentjev (1963:367).
- Sphaerodactylus lineolatus* (part)—Barbour (1921:238), Dunn (1940:189), Villa (1983:28).
- Sphaerodactylus lineolatus*—Savage (1973a:10).

DIAGNOSIS.—A moderately large sphaerodactyl, maximum size of male, 32.5 mm. SVL, female, 32.6 mm. SVL. Dorsal trunk scales strongly keeled (knobby), small, homogeneous, 48–67 axilla-groin. Ventrals 30–40. Scales around midbody 67–87. Ventral count averages 59.3% of dorsal count. Parietal scales keeled. One supranasal, separated from other by one or rarely two small internasals. Rostral with long median cleft; small notch behind, filled by as much as one small scale. Fourth supralabial lies below anterior half of eye; fourth infralabial below center of eye. Subcaudal scales up to three times width of supracaudals, alternately arranged. Escutcheon confined to posterior third of venter, composed of 38–79 scales. Neck and body crossed by four bands, dark in young, faded, but still well-defined in adults. Head of adult males striped, spotted or reticulated with lemon yellow; adult females with numerous, fine, longitudinal lines on nape.

Sphaerodactylus homolepis differs from *S. argus*, *S. glaucus* (smooth scaled), *S. graptolaemus*, and *S. millepunctatus* in lacking a median row of enlarged subcaudal scales. Unlike *S. dunni*, the top of the snout does not protuberate and the dorsal trunk scales are not subequal to the ventrals in *S. homolepis*. *Sphaerodactylus lineolatus* differs in its generally higher dorsal scale count (62–81), coloration (Fig. 1), escutcheon size (Fig. 5), and subcaudal scale configuration (Fig. 4).

DESCRIPTION AND VARIATION.—A moderately large sphaerodactyl; adult males and females measure 24.5–32.5 mm. SVL (\bar{x} = 28.5, s = 2.18, N = 26) and 24.5–32.6 (\bar{x} = 29.6, s = 1.83, N = 33), respectively; smallest specimen 15.0 mm. Snout-ear distance 23.1–25.4% of

SVL (\bar{x} = 24.0, s = 0.81, N = 10). Head width 58.3–64.6% of snout-ear distance (\bar{x} = 61.4, s = 2.01, N = 10). Head depth 40.3–47.7% of snout-ear distance (\bar{x} = 43.5, s = 2.06, N = 10). Snout long, length equal to distance from ear to center of eye. Sides of snout converge, forming 39.5–43.5° angle (\bar{x} = 41.9, s = 1.47, N = 10); tip rounded. Original tail 95–108% of SVL (\bar{x} = 99.2, s = 5.44, N = 6). Rostral with long median cleft and small posterior indentation filled with no more than one small scale. Supranasal scale large, in broad contact with nostril, separated from first supralabial by small posterior supranasal and single postnasal behind nostril, and by rostral anteriorly. Space between supranasal scales narrower than supranasal; one internasal, infrequently two. Snout scales flat, keeled, 9–10 orbit-rostral, four per IOW. Scales narrow between eyes. Parietal surfaces and nape covered with keeled scales, 5–6 per IOW. Fourth supralabial elongated, underlying anterior half of eye. Fourth infralabial below center of eye; first infralabial largest, its length 1.75–2 times IOW. Mental large, as long as wide; its borders with first infralabials slant or curve backward from mouth. Postmentals polygonal, rounded; 2–4 border mental. Gular scales smooth, granular, 5–6 per IOW.

Dorsal scales of trunk rhomboid, strongly keeled, juxtaposed, somewhat raised, with free posterior edges, ca. four per IOW, 48–67 (\bar{x} = 58.4, s = 4.15, N = 66) axilla-groin. Lateral scales like dorsals. Ventrals two per IOW, 30–40 (\bar{x} = 34.5, s = 2.45, N = 67). Ventral counts 50.8–75.5% of dorsal counts (\bar{x} = 59.3, s = 5.04, N = 66). Scale rows around midbody 67–87 (\bar{x} = 75.9, s = 4.41, N = 64). Escutcheon large, elliptical, circular, confined to posterior third of venter, composed of 35–79 scales (\bar{x} = 58.7, s = 10.13, N = 25), 7–12 by 6–7. Escutcheon size and SVL are correlated (Fig. 5; r = 0.615, N = 25, P > 0.01); trend also evident in a local sample from Río Frío, Costa Rica. Supracaudal scales rhomboid, flat, imbricate, 2–3 per IOW, keeled at base for a head length, smooth distally; alternating. Subcaudal scales as much as three times width of supracaudals; similar in form to ventrals, neither aligned in longitudinal median row, nor widened. Limb squamation similar to that of trunk; scales imbricate on prefemoral surfaces. Digit scales smooth, subimbricate, transversely expanded into lamellae below, 10–12 (\bar{x} = 11.2, s = 0.63, N = 37) under fourth toe.

Color in life taken from a transparency of a male (CRE 3741) photographed by Wayne Van Devender. Head with brilliant lemon-yellow oblong spots edged with black on tawny light brown. Trunk light buff brown, darkening posteriorly, then grading into ochraceous yellow on tail. Limbs colored like trunk, with creamy yel-

low spots; fingers banded. Head may be striped, spotted, or mottled. Head coloration ends abruptly at the nuchal cross-band. Usually, pale dorsum of trunk and tail of male has small brown spots covering one to three scales each. Chin with fine reticulation.

Juveniles cream, boldly crossed by dark brown bands at nape, shoulder, midtrunk and pelvis; about five dark bands on tail (Fig. 1D). Juvenile bands fade with age, from midbody outward. Bands usually do not disappear altogether in adults, but persist with the same well-defined edges as in juveniles, while nearly matching ground color (Fig. 1C).

Females with faint cross-bands, dorsum finely variegated. A series of a dozen light pinstripes, alternating with darker lines, begin at occiput and disappear over scapula near midline, shortening to mere dots on side of neck (Fig. 13). Not all preserved specimens show these pinstripes.

DISTRIBUTION.—Caribbean coast of lower Central America, from central Panamá to southern Nicaragua.

REMARKS—The holotype is a desiccated juvenile missing some limbs. It clearly has strongly keeled dorsal scales, not smooth ones as stated by Cope (1886).

This species is similar to *S. lineolatus*. The character most useful for differentiating the two is the form of the dorsal scales. In *S. lineolatus*, there is a narrow ridge on a relatively flat scale. The keel is high-peaked or tectiform in *S. homolepis*. The number of escutcheon scales, in relation to SVL, tends to be large in *S. homolepis*. *Sphaerodactylus homolepis* and *S. lineolatus* are viewed as distinct species; however, there is a possible zone of intergradation or hybridization between the two, as discussed under *S. lineolatus*.

SPECIMENS EXAMINED.—COSTA RICA: CARTAGO: Peralta, Tunnel Camp, Lake Bonilla (KU 40508–9); vic. Turrialba (MVZ 79788). HEREDIA: La Selva, 30–60 m. (CRE 69a–b, 837, 913, 3741, 8405, 8462, 8817); Río Frío, Standard Fruit Co., 10°20'N, 83°53'W, 101 m. (UF 30536, 30805, 30893, 30916–17, 30950, 31010, 31029, 31050–51, 31066, 31180, 31250, 31305, 31451, 31524, 31615, 32216, 32457, 52486). LIMÓN: Batán (KU 40506–7); La Castilla, west bank Río Reventazón, 3 km. N Carmen, 4 km. SW Golden Grove (ANSP 23754, 24582); Los Diamantes (UMMZ 117608); Estrella Valley, Atalanta Farm (ANSP 21464); 4.8 km. S Jiménez, Los Diamantes, 230 m. (CRE 8406); Finca La Lola (UF 7691); Lari (MCZ 19483); Limón (UF 50245); Limón [on bananas in Boston] (USNM 69382); Siquirres (UMMZ 137033); Tortuguero (UF 10304, 10519, 12057, 50246–47); ca. 29 km. (by air) W Tortuguero (LACM 130942); Tortuguero,

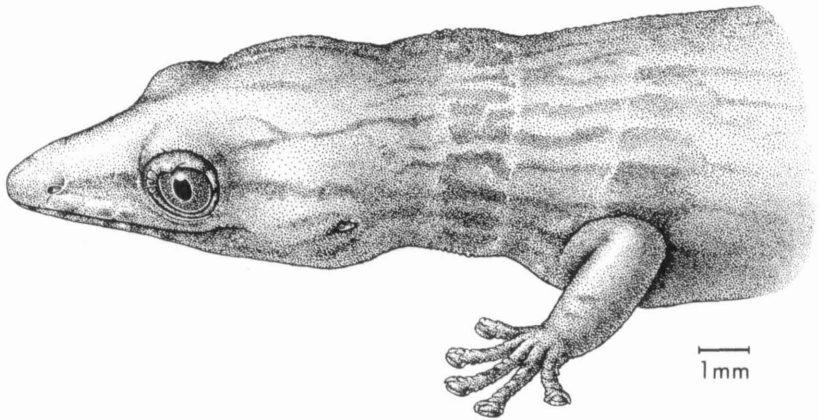


FIG. 13. Head and anterior body color pattern of *Sphaerodactylus homolepis* (UF 31615—adult female). Note the fine longitudinal lines on the neck.

Green Turtle Camp (AMNH 95084). PROVINCE UNKNOWN: (USNM 69426, 71475, 101833).

NICARAGUA: RÍO SAN JUAN: [restricted type-locality: between El Castillo and San Juan del Norte, along the Río San Juan and its tributaries] (USNM 14207).

PANAMÁ: BOCAS DEL TORO: 3.2 km. NW Almirante, 10 m. (KU 113095); mouth Río Cahuita, 1 m. (KU 113101); Careening Cay, 2 m. (KU 113099); Río Coclé del Norte (USNM 129839); Punta de Peña [village nr. Pico de Chiriquí, ca. 8°55'N, 82°11'W] (GML [=USNM 38704]; MCZ 13455; USNM 38699–700, 38702–3, 38705–6).

Sphaerodactylus dunni Schmidt

Figs. 14–15, 17–18

Sphaerodactylus dunni Schmidt (1936:46). Type-locality: Honduras: Naco River, near Cofradía. Holotype: MCZ 32199. Collector: R. E. Stadelman.

Sphaerodactylus dunni—Peters and Donoso-Barros (1970:252), Hahn (1971:111), Meyer and Wilson (1971:109; 1973:12), Schwartz (1973:142.2).

DIAGNOSIS.—A small sphaerodactyl reaching 27.7 mm. SVL. Dorsal trunk scales large, homogeneous, keeled, 30–36 axilla-groin, three per IOW. Ventrals 26–29, averaging 81.6% of dorsal count. Snout dorsal surface protuberates. Supraocular spine lies at or behind mid-

eye. Scales around midbody 61–71. Two supranasals; anterior ones separated by two or three internasals, however, anterior supranasals may be fused to rostral (Fig. 14). Rostral small relative to other species; only slightly visible from above with short median cleft; may be intruded behind by part of a small scale. Third supralabial lies below anterior half of orbit. Third infralabial below center of eye. Width of largest subcaudal scale equal to width of 2–2.5 supracaudals. Subcaudals alternating, not aligned in a median row. Escutcheon weakly hypertrophied, hemielliptical or bell shaped, extending subfemorally or not; hypertrophication does not reach edge of scale (Fig. 15). With a wide dark collar and light narrow curving cross-bands on dorsum.

The very large dorsal scales, three instead of four supralabials, protuberating top of snout, and position at or behind mideye of the supraocular spine are all characteristics unique to *S. dunni* among the Middle American sphaerodactyls.

DESCRIPTION AND VARIATION.—Five males and two females. A small sphaerodactyl 21.3–27.7 mm. SVL. Head dimensions for the type, LACM and LSUMZ specimens (N=5) are as follows: Snout-ear distance 20.1–23.3% of SVL (\bar{x} = 22.0, s = 1.28); head width 63.8–69.4% of head length (\bar{x} = 67.4, s = 2.27); head depth 43.9–50.0% of head length (\bar{x} = 47.5, s = 2.50). Snout short; length (orbit-tip) not exceeding distance from ear to posterior edge of eye. Sides of snout converge at 41.5–46° angle; tip blunt, rounded in dorsal view, truncate in lateral view. Top of snout protuberates, appearing convex from side view, then slightly depressed above the blunt ridge crossing rostral. Extrabrillar fringe extends posteriorly to or behind vertical axis of pupil. Rostral with little dorsal surface, short median cleft may be present, not intruded by small scales. Two supranasals (anterior scale may be fused to rostral), anterior larger, separated from other anterior supranasal by 2–3 internasals in space as broad as supranasal. Anterior supranasals frequently fused to rostral as in fig. 14. Two postnasals. Snout scales slightly thickened, keeled, 9–11, 4–5 per IOW. Parietal surfaces and occiput covered with keeled granules, 5–6 per IOW. Third supralabial elongated, lying below anterior half of orbit. Third infralabial below anterior half of spectacle. First infralabial up to 1.6 times IOW. Mental large, its borders with first infralabials slant backward from mouth. Postmentals polygonal, rounded; two border mental. Gular scales smooth, granular, 4–5 per IOW. Scales on side of neck swollen and keeled, knobby.

Dorsal and lateral trunk scales homogeneous, rhomboid, flat, keeled, strongly imbricate, three per IOW, 30–36 axilla-groin (\bar{x} = 33.7, s = 2.06, N = 7). Ventrals flat, smooth, 2–2.5 per IOW, 26–

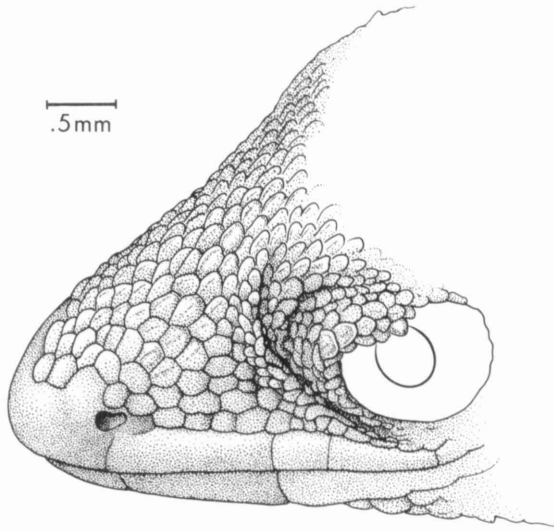


FIG. 14. Head squamation of *Sphaerodactylus dunni* (LACM 47303).

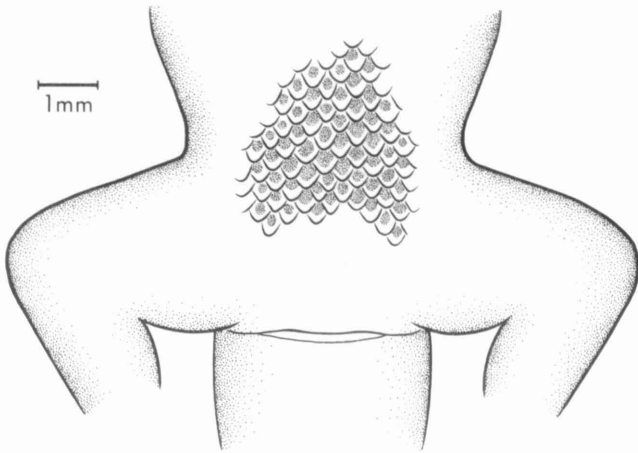


FIG. 15. Escutcheon of *Sphaerodactylus dunni* (LACM 47302).

29 axilla-groin (\bar{x} = 27.4, s = 1.13), 74.3–93.3% of dorsal count (\bar{x} = 81.6, s = 5.78). Scales around midbody 61–71 (\bar{x} = 64.7, s = 3.61, N = 6). Escutcheon on posterior third of venter, about 6–7 by 10, with 58–59 total scales in LACM 47302–3. Hypertrophication weak, not reaching edge of escutcheon scale. Supracaudal scales keeled for almost head length proximally, smooth distally, similar to dorsals. Subcaudal scales as wide as 2–2.5 supracaudals, arranged alternately from whorl to whorl. Limb squamation consistent with trunk, but posterior surfaces bear small granules. Digit scales smooth, imbricate, transversely expanded into lamellae below, 9–10 under fourth toe.

Light band crosses occiput; light, narrow curved bands connected by a light vertebral stripe regularly cross dorsum, fading on anterior trunk into uniform medium brown. Neck ground color dark brown. Light occipital band with temporal extensions to eye. A similar band occurs on canthus and rostral ridge. Light head bands bordered below by dark brown. Six white, chevron-shaped, dark-bordered bands on side of and below head, sometimes broken into series of spots. Color darker in males.

DISTRIBUTION.—Lowlands of northern Honduras.

SPECIMENS EXAMINED.—HONDURAS: ATLÁNTIDA: 11.3 km. S La Ceiba (LACM 47302–4); COLÓN: mts. S Trujillo (CM 64529); mts. above Trujillo, 600–700 m. (LSUMZ 22450). CORTÉS: Río Naco, nr. Cofradía (MCZ 32199); mts. W San Pedro Sula on “Carocoil” rd. (CM 64528).

Sphaerodactylus argus Gosse

Fig. 16

Sphaerodactylus argus Gosse (1850).

Sphaerodactylus lineolatus (part)—Breder (1946:426), Lee (1980:57).

DIAGNOSIS (abstracted, in part, from Thomas, 1975).—A moderate to large sphaerodactyl, reaching 33 mm. SVL; modal size for males 29 mm., females 31 mm. Dorsal trunk scales moderate in size, slightly swollen, broadly angulate to rounded on posterior edges, keeled, and weakly imbricate, dorsals (i.e., dorsolaterals) 38–50. Ventrals 26–37. Scales around midbody 57–73. Parietal scales keeled. Two supranasals, anterior pair separated by 0–3 internasals. Rostral with long median cleft and small posterior notch intruded by part of a small scale. Fourth supralabial below anterior half of eye; fourth infralabial below center of eye. Subcaudal scales enlarged, may be widened 3–4 times

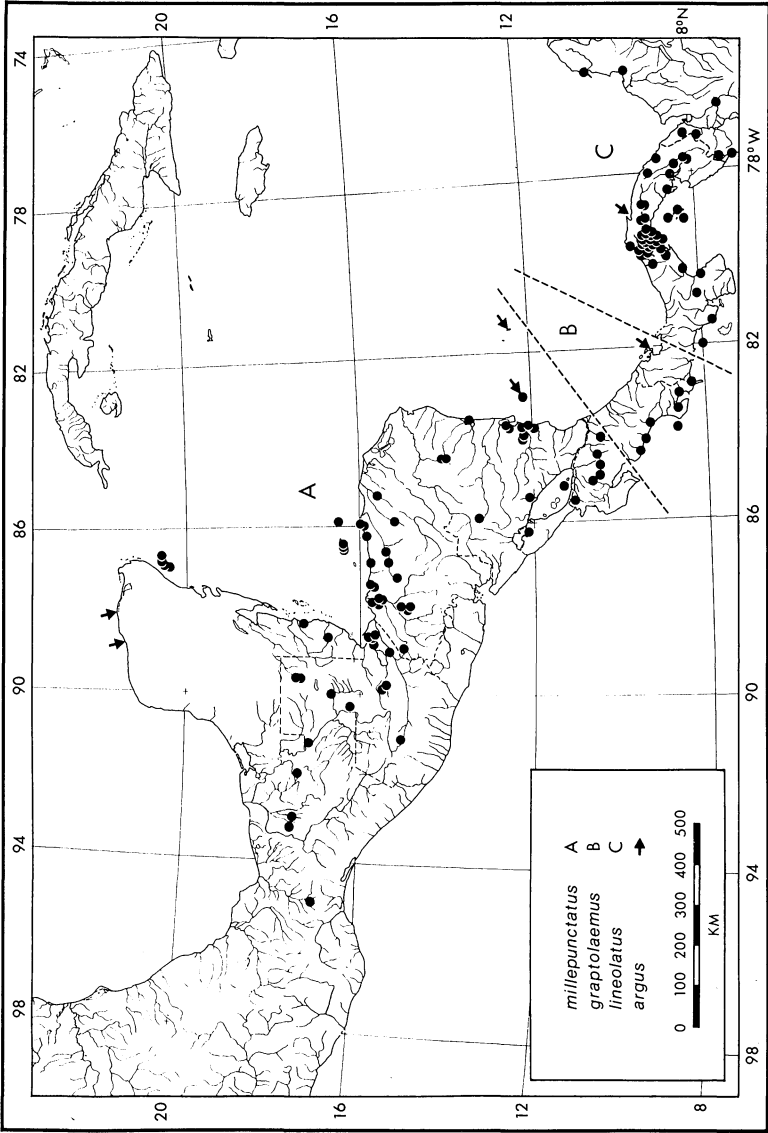


FIG. 16. Range map for *S. millepunctatus* (A), *S. graptolaemus* (B) and *S. lineolatus* (C). The Middle American records for *S. argus* are denoted by arrows.

width of supracaudals; aligned in median series. Escutcheon bell shaped with moderate-sized central area and broad extensions well onto thighs, often to knee. Juvenile color pattern consists of a series of light longitudinal stripes on a dark ground color. Light stripes of juvenile become broken in adults to form rows of small ocelli which often disappear posteriorly in a fine dorsal and lateral reticulation.

Sphaerodactylus argus is distinguished from *S. glaucus* by having keeled dorsal scales; from *S. dunni*, *S. homolepis*, and *S. lineolatus* by having a median row of subcaudals; from *S. graptolaemus*, *S. homolepis*, and *S. lineolatus* by having two supranasals rather than one; and from *S. millepunctatus* by the color-pattern, which contains no dark suprapelvic or pectoral blotches.

DISTRIBUTION.—Jamaica, including the Pedro Cays (Northeast Cay); Isla San Andrés; Islas de Maíz; scattered localities on Cuba and two cays off its south coast, Cayo Cabeza del Este in the Jardines de la Reina *cayeria* and Cayo Levisa near Santa Cruz del Sur; the Bahamas (North Bimini and New Providence); and Key West, Florida—Thomas (1975). The known range is extended to include scattered localities along the Caribbean side of Bocas del Toro and San Blas in Panamá, and the Yucatán peninsula of México.

REMARKS.—This is the first published report of *Sphaerodactylus argus* from continental Middle America, where it appears to be well established.

SPECIMENS EXAMINED.—COLOMBIA: SAN ANDRÉS Y PROVIDENCIA: Is. San Andrés (AMNH 91715–16; UMMZ 173075–80).

MÉXICO: YUCATÁN: Dzilam Bravo (KU 157140); Río Lagartos (KU 157109–39).

NICARAGUA: Zelaya: Is. Maíz Grande, 30 m. (AMNH 97023–29; KU 85627; UMMZ 173055–74); Is. Maíz Grande, N end (KU 101378).

PANAMÁ: BOCAS DEL TORO: Cayo Zapatilla Chica, 1 m. (KU 113100). SAN BLAS: Arguantupo (MCZ 149408); Caledonia [8°55'N, 77°42'W (*fide* C. W. Myers, pers. comm.)] (AMNH 60301, 65299); Corbisquí (MCZ 145007–16, 145019, 145021, 145023, 145025–33, 145035, 145038); Nalunega (MCZ 149409–98; UMMZ 145838–42, 145934–35, 146880, 147002, 155791–95); Wichi Walla (UMMZ 135407); locality unknown (UMMZ 155801).

RELATIONSHIPS

Sphaerodactylus dunni, *S. graptolaemus*, *S. glaucus*, *S. heliconiae*, *S. homolepis*, *S. lineolatus*, *S. millepunctatus*, *S. molei*, *S. pacificus*, and *S. scapularis* are considered a Middle-South American endemic group

because each species shares various specialized conditions with other species restricted to those areas (see individual species descriptions above for documentation). However, we have been unable to discover a single character that would unambiguously unite all of them as a monophyletic group. Therefore, more than one line of evolution from the Caribbean is implied. Only the reduction of the escutcheon below the legs provides evidence of the common ancestry of all those species, excluding *S. glaucus* and *S. millepunctatus*. Within that larger assemblage, the presence of a single supranasal scale diagnoses the *lineolatus* group (*S. graptolaemus*, *S. homolepis*, *S. lineolatus*, *S. pacificus*, *S. scapularis*). *Sphaerodactylus dunni* and *S. molei* share much reduced interclavicle arms, while those two species, plus the *lineolatus* group, exhibit a reduced clavicle fenestra. These observations and the corresponding phylogenetic hypotheses deduced from them are summarized in fig. 18.

The peculiar pattern of alternating small and large subcaudals is characteristic of all endemics (Fig. 4) except *S. graptolaemus*, *S. glaucus* and *S. millepunctatus* (Fig. 7). The distribution of this character can be interpreted in either of two equally parsimonious ways on the phylogenetic hypothesis illustrated in fig. 18; the derived state is convergent in the *dunni-molei* and *lineolatus* group clades, or *S. graptolaemus* exhibits an evolutionary reversal. We are unaware of any evidence on which to base a choice between these alternatives.

The phylogenetic hypothesis presented in fig. 18 must be considered highly speculative. We have been unable to corroborate any of the synapomorphies employed with other shared-derived conditions. Secondly, none of the shared-derived conditions are unique among gekkos, and in some cases one must assume independent evolution within the genus *Sphaerodactylus*. Perhaps most important is the high degree of individual variation observed, even in the skeletal characters which have been otherwise viewed as relatively conservative and thus good indicators of genealogy (Kluge, 1975). All of the characters considered, but especially those scored from the skeletal system, are more variable than in their Caribbean counterparts. The nature of this variation will be investigated more fully in the context of intergeneric relationships among sphaerodactylines (Kluge, in prep.). Russell's (1972:243) claim that the Caribbean radiation of *Sphaerodactylus* was derived from a Middle American stock seems to be unfounded.

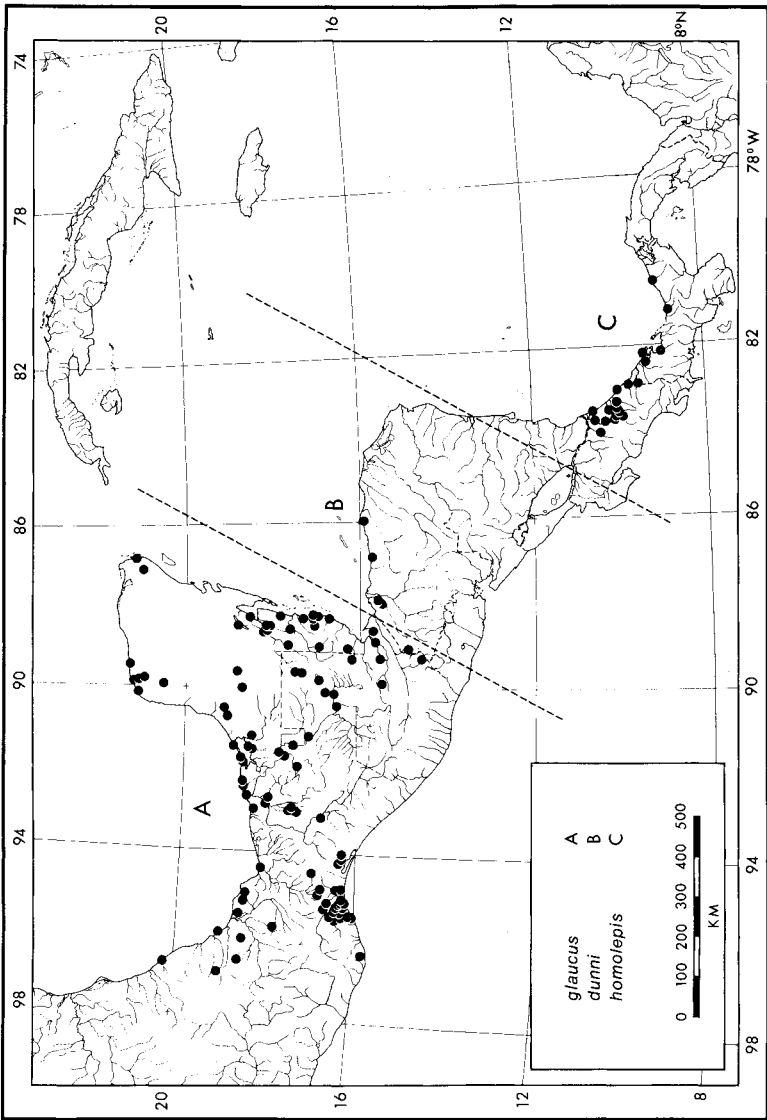


FIG. 17. Range map for *S. glaucus* (A), *S. dunni* (B) and *S. homolepis* (C).

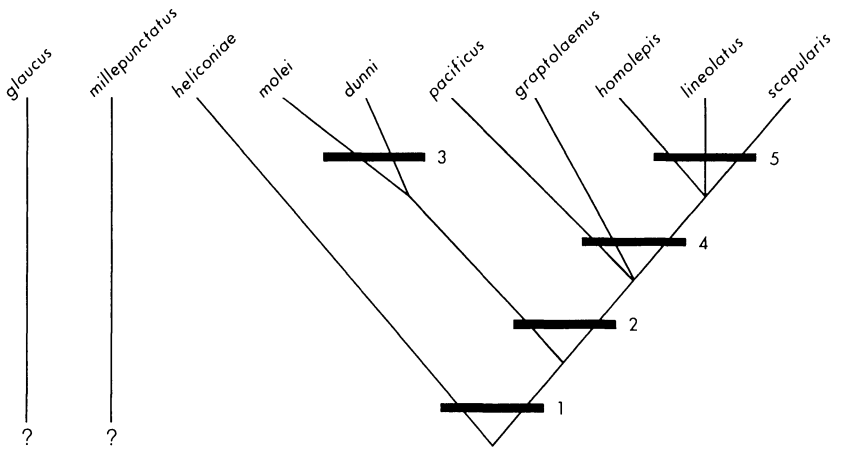


FIG. 18. Cladistic relationships among Middle-South American endemic sphaerodactyls. The synapomorphies are as follows: 1—reduction of subfemoral escutcheon scales in males; 2—reduced clavicle fenestra; 3—reduced interclavicle arms; 4—a single supranasal scale; 5—juveniles with conspicuous body bands. The sister group affinities of *S. glaucus* and *S. millepunctatus* are unclear.

DIAGNOSTIC KEY TO MIDDLE AND SOUTH AMERICAN *SPHAERODACTYLUS*

1. Narrow middorsal row of fine granules separates large, tectiform, dorsal scales. To 39 mm. SVL (see Wilson and Hahn, 1973:106). Islas de la Bahía, Honduras..... *rosaurae*
 Without a middorsal zone of small scales between large tectiform scales 2
2. Large species, adult SVL exceeding 40 mm.; supranasals single, small with wide gap in-between (separated by 2–4 small scales). Also, dorsals strongly keeled; escutcheon abdominal, small (10–16 scales); median subcaudals alternate; dorsal pattern crudely blotched in adult, plain in juveniles. Endemic to Isla del Coco, Costa Rica..... *pacificus*
 Small species, not exceeding 34 mm. SVL; pattern not as described above 3
3. Snout strongly protuberate, dorsally convex in profile; eye spine behind mideye. Also, dorsal scales keeled, large (30–36 axilla-groin); subcaudals arranged alternately; two supranasals or one when anterior supranasal is fused to rostral. Northern Honduras *dunni*
 Snout flat, sloping straight from eyes to rostral; eye spine lies anterior to mideye 4
4. Supranasal single; escutcheon abdominal..... 5
 Two supranasals; escutcheon abdominal or abdominal and subfemoral 8
5. Median subcaudals aligned in series; no dark bands in dorsal pattern. Also, dorsals and parietals keeled; dorsal count 51–63; escutcheon abdominal with 22–61 total scales. Southern Costa Rica to Pacific western Panamá *graptolaemus*
 Subcaudals not in straight series; young banded 6

6. Dorsals smooth; six dark bands or their remnants on head and body. Also, subcaudal scales alternate; dorsal count 70–81. Northwestern Ecuador to southwestern Colombia *scapularis*
Dorsals keeled; four dark bands on head and body of juveniles especially 7
7. Dorsal scales strongly keeled, knobby; parietal scales keeled; subcaudals alternate; dorsal count 48–67; escutcheon with 38–79 total scales; bands of juvenile persist in adult, faded but definite. Caribbean versant of southern Nicaragua to western Panamá *homolepis*
Dorsal scales moderately keeled, parietals usually without keels; dorsal count 62–81; subcaudals arranged in the repeating sequence of a small, a large and a pair of small scales; escutcheon with 20–52 total scales; broad dark crossbands of juveniles become indefinite and are replaced by variegation in adults. Pacific western Panamá to northwestern Colombia *lineolatus*
8. Dorsal scales smooth. Dorsal count 46–71; median subcaudals aligned in series; escutcheon of 19–97 total scales, extending to knees. Southern México to extreme northwestern Honduras *glaucus*
Dorsal scales keeled 9
9. Space between anterior supranasals as wide as a supranasal; rostral deeply notched behind, containing 1–3 small scales; escutcheon abdominally confined 10
Space between anterior supranasals much narrower than a supranasal; rostral notch shallow or absent; escutcheon may extend to knee 11
10. Subcaudals alternate; escutcheon small (13–38 total scales); dorsal count 63–83; continuous light dorsolateral stripes present, faded in males with black and yellow-white striped heads. Venezuela, Trinidad, Tobago, and Guyana. *molei*
Median subcaudals aligned in series; escutcheon huge (94–154 total scales); dorsal count 62–80; dorsolateral series of spots in females; in male, trunk and tail reticulated, head orange. Lowlands immediately west of the Santa Marta Mountains of northern Colombia *heliconiae*
11. Dorsal scales large (18–36 axilla-groin); three supralabials to below eye; dorsum brownish gray with small brown spots; nape with large dark brown spot between smaller light spots. Cuba, Bahamas, Florida, pan-Caribbean. One specimen recorded from northwestern Colombia (Harris, 1982). *notatus*
Dorsals small to moderate (38–74 axilla-groin); four supralabials to below eye. 12
12. Dorsals 38–50 axilla-groin; young with six distinctive, light stripes on head and nine running length of body, changing to rows of ocellar spots on a densely dark-spotted dorsum in adults; fine spotting on limbs. Coastal sites in northern Yucatán, México; Bocas del Toro and San Blas, Panamá, besides Jamaica and other Caribbean islands. *argus*
Dorsals 47–74 axilla-groin; young usually with prominent dark markings on body near forelimbs, a large, round, dark spot above pelvis, and feeble head lines on a uniform tan background; adults finely speckled to strongly variegated with dark color; head of male may become boldly marked, but never with rows of ocellar spots; three large, light spots on each limb. Isthmus of Tehuantepec to northern Costa Rica, and Cozumel, and Roatán, Guanaja, and Maíz Grande islands *millepunctatus*

SUMMARY

Sphaerodactylus dunni, *S. glaucus*, *S. homolepis*, *S. lineolatus*, *S. millepunctatus*, *S. pacificus*, and *S. rosaurae* have been confirmed as valid Middle American species. *Sphaerodactylus continentalis*, *S. mertensi*, and *S. torquatus* were referred to the synonymies of *S. millepunctatus*, *S. homolepis*, and *S. glaucus*, respectively. In addition, a new species, *S. graptolaemus*, was described from the southern Pacific versant of Costa Rica and adjacent Panamá, and the widespread Antillean *S. argus* was recorded from several Caribbean coastal localities along the mainland. Number of escutcheon scales was shown to be correlated with SVL in *S. glaucus*, *S. homolepis* and *S. lineolatus*. *Sphaerodactylus glaucus* exhibited a correlated pattern of geographic variation in dorsal and midbody scale counts, and number of dorsal scales was found to vary clinally in *S. millepunctatus*. All Middle and South American species, except *S. glaucus* and *S. millepunctatus*, appear to form a monophyletic group. A diagnostic key to Middle and South American species is provided.

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