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SYSTEMATICS OF THE LIZARDS OF THE GEKKONID GENUS
PHYLLODACTYLUS OF MAINLAND SOUTH AMERICA

By JAMES R. DIXON AND RAYMOND B. HUEY

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SYSTEMATICS OF THE LIZARDS OF THE GEKKONID GENUS PHYLLODACTYLUS OF MAINLAND SOUTH AMERICA

By JAMES R. DIXON¹ AND RAYMOND B. HUEY²

ABSTRACT: A brief description of the habitat of species of *Phyllodactylus* of mainland South America is presented. Microhabitat preferences are given for each species where possible. Little or no microhabitat information is available for *P. heterurus*, *sentosus*, and *clinatus*. Four species, *P. angustidigitus*, *gerhropygus*, *microphyllus*, and *sentosus* are primarily terrestrial and allopatric in distribution. Nine species, *P. clinatus*, *dixonii*, *inaequalis*, *interandinus*, *johnwrighti*, *kofordi*, *lepidopygus*, *pumilus*, *reissi*, and *ventralis* are scansorial and only *johnwrighti*, *ventralis*, and *dixonii* are not found sympatric with one or more of the other scansorial species. Where three or more species are sympatric, there is little overlap in daytime retreats and foraging areas.

One egg is laid per clutch by most species of *Phyllodactylus* of mainland South America except *reissi*, which lays two eggs. Information on clutch size is not available for *P. heterurus*, *sentosus*, and *clinatus*. Communal egg laying appears to be common among most species, including such sympatric species as *P. interandinus* and *reissi*, *kofordi* and *reissi*.

Species of *Phyllodactylus* appear to have specific adaptations to their microhabitat. Enlarged terminal digital lamellae, dorsoventrally compressed head and body, and lateral nostrils characterize species of *Phyllodactylus* from a boulder microhabitat; small terminal digital lamellae, round body and head, dorsolateral valvular nostrils for species from a sand microhabitat; small terminal digital lamellae with enlarged claw, slim body and head, dorsolateral valvular nostrils for species from shell beaches. Depending upon the degree of scansorial or terrestrial behavior some species of *Phyllodactylus* are intermediate in the above adaptations.

Distribution maps and photographs are given for each species, except *P. heterurus*, and a gazetteer of important localities is presented.

Of the holotypes and syntypes for species described from the mainland of South America, ten (*dixonii*, *inaequalis*, *lepidopygus*, *magister*, *microphyllus*, *nigrofasciatus*, *phacophorus*, *pumilus*, *reissi*, and *ventralis*) are extant and eight have been examined. Seven new species (*angustidigitus*, *clinatus*, *interandinus*, *johnwrighti*, *kofordi*, *pumilus*, *sentosus*) are described herein and nine older names (*abrupteseriatus*, *baessleri*, *guayaquilensis*, *lobensis*, *magister*, *nigrofasciatus*, *phacophorus*, *underwoodii*, *variegatus*) are relegated to the synonymy of other species.

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INTRODUCTION

The leaf-toed geckos, genus *Phyllodactylus*, form two distinct geographic units in South America, a northeastern group in Colombia, Venezuela and the Caribbean Islands, and a western group in Ecuador (including the Galapagos Islands), Peru, and Chile. A study of the northeastern representatives was completed by Dixon (1962, 1964a). The present work treats the systematics and biology of the mainland South American *Phyllodactylus*. Although the Galapagos Islands species are evolutionarily close relatives to the mainland species of western South America, they are a special problem and will be reported on at a later date.

The earliest description of a species for the mainland of South America was by Wiegmann (1835) for *P. gerrhopygus* and the most recent by Rivero-Blanco and Lancini (1968) for *P. dixonii*. A total of 19 species have been described, ranging from the coast and mountain areas of Ecuador to Chile, including the upper Amazon Basin of northwestern Peru in western South America; from the lowlands and foothills of eastern Colombia to central Venezuela in eastern South America.

A common Mexican and Central American species, *P. tuberculosus*, described by Wiegmann (1835), has also been reported in the literature from Ecuador, Peru, the Galapagos Islands, and the Greater Antilles. The distribution of this species is Mexican and Central American (Dixon, 1960), and specimens on the mainland and islands of South America to which this name has been misapplied represent populations of *P. reissi*, *P. darwini*, and *P. wirshingi*.

Individual species were studied and described by Wiegmann (1835), Tschudi (1846), W. Peters (1862), Cope (1876, 1877), Werner (1901, 1907, 1910, 1912), and Noble (1924). Short notes on distribution, habitat and taxonomy of mainland South American species were given by Parker (1935), Taylor (1942), Codoceo (1950), Titschack (1951), Yañez (1951), Dixon (1962, 1964a), J. Peters (1967), Donoso-Barros (1966), and Rivero-Blanco and Lancini (1968).

As a group, the mainland South American species were studied by Boulenger (1885) and Werner (1912), both of whom published a key to the arid and tropical American species known at the time. Burt and Burt (1933) published a preliminary checklist of lizards of South America. Wermuth (1965) published a world checklist of the genera, species, and subspecies of the family Gekkonidae, and Vanzolini (1968a) published a paper on the geographic distribution of South American Gekkonidae. Vanzolini (1968b) also published a key and list of Gekkonidae known to occur in Brazil, and included a list of the species of *Phyllodactylus* known to occur in South America. Mechler (1968) published a key, descriptions, and maps for all gekkonids in Colombia.

Some of the latter studies contain errors in species determination, through the uncritical acceptance of publications of earlier workers who did not have

adequate knowledge of the distribution and ecology of the species. With some of these problems in mind, a study of the genus was initiated by one of us (Dixon) in 1957. Recent collections of *Phyllodactylus* by Huey in 1967 and 1968, and by Dixon and Wright in 1968, from the coast and upper Amazon Basin of Peru and an examination of extant syntypes and holotypes of South American species has provided the necessary material to complete this study.

A detailed study of the sympatric relations of *P. kofordi*, *P. microphyllus*, *P. reissi*, and *P. clinatus* will be presented by one of us (Huey) at a later date.

TYPE MATERIAL

Of the 19 available names for mainland South American species of *Phyllodactylus*, only nine have extant type material that has been examined by us: *lepidopygus*, *phacophorus*, *reissi*, *inaequalis*, *microphyllus*, *nigrofasciatus*, *magister*, *ventralis*, and *dixonii*.

The remaining 10 typical series are either definitely destroyed or lost. The museums in Hamburg and Dresden were seriously damaged during the fire bombings of the second world war. Among type material destroyed in the Dresden Museum were the nine syntypes of *P. variegatus* and the holotype of *P. baessleri*. The Hamburg Museum lost two syntypes each of *P. abruptereriatus* and *P. guayaquilensis*, and type material (if any existed) of *P. lobensis* (nomen nudum). The syntypes of *P. gerrhopygus*, reported to be housed in the Berlin Museum, are lost (Wermuth, pers. comm.). The holotype of *P. heterurus*, housed in the School of Medicine, University of Chile, was destroyed by a fire in the early 1950's (Capurro, pers. comm.).

Fortunately, Donoso-Barros (1947) was able to examine the type of *P. heterurus* in detail prior to its destruction by fire. However, some of the early type descriptions by Werner (1912) were brief and failed to give a detailed description that could be used to identify his species with certainty. Therefore, our analyses of his original descriptions and our subsequent synonymies based on these descriptions may be in error.

A problem related to the loss of types is knowledge of the exact type locality for some species. Werner (1912) gives the type locality for *P. abruptereriatus* as "probably Brazil." Members of this genus have never been found in Brazil and we assume, as have earlier workers (e.g. Burt and Burt, 1931), that the type series probably came from Ecuador or northern Peru. The type description clearly describes individuals of *Phyllodactylus reissi* Peters in these areas. Tschudi's (1846) original descriptions of *P. lepidopygus* and *P. phacophorus* gave only the type locality for the former species (Chorillos, Peru). The only statement made on the type locality of the latter species was "a wooded region." Werner's (1901) description of *P. baessleri* gave the town of Chanchamayo, Peru, as the type locality. Several towns of that name were located in west central and southern Peru. Most of these towns are sufficiently low in elevation to sustain populations of *Phyllodactylus*, but only two species are known to occur in the above areas, *P. gerrhopygus* and *P. lepidopygus*.

The only known populations fitting Werner's description are found 1600 km NW of the nearest town named Chanchamayo. Therefore, the type locality of *P. baessleri* is presumed to be in error.

These and other problems have been responsible for the misapplication of species names in a number of publications on *Phyllodactylus* over the past 100 years. Consequently, we present the following table of the chronological synonymy of sixty-one specific names proposed for North, Central, and South American species.

TABLE 1

Chronological synonymy of sixty-one specific names proposed for the genus *Phyllodactylus* from North, Central and South America

<i>Date, original name and author</i>	<i>present name</i>
1830 <i>pulcher</i> Gray	<i>pulcher</i>
1835 <i>tuberculosis</i> Wiegmann	<i>tuberculosis</i>
1835 <i>gerrhopygus</i> (Wiegmann)	<i>gerrhopygus</i>
1836 <i>gymnopygus</i> Dumeril & Bibron	<i>gerrhopygus</i>
1846 <i>lepidopygus</i> (Tschudi)	<i>lepidopygus</i>
1846 <i>phacophorus</i> (Tschudi)	<i>lepidopygus</i>
1862 <i>reissi</i> Peters	<i>reissi</i>
1862 <i>spatulatus</i> Cope	<i>pulcher</i>
1862 <i>julieni</i> Cope	<i>julieni</i>
1863 <i>unctus</i> Cope	<i>unctus</i>
1863 <i>xanti</i> Cope	<i>xanti</i>
1869 <i>galapagoensis</i> Peters	<i>galapagoensis</i>
1875 <i>ventralis</i> O'Shaughnessy	<i>ventralis</i>
1876 <i>inaequalis</i> Cope	<i>inaequalis</i>
1876 <i>microphyllus</i> Cope	<i>microphyllus</i>
1877 <i>nigrofasciatus</i> Cope	<i>lepidopygus</i>
1887 <i>martini</i> Van Lidth de Jeude	<i>martini</i>
1889 <i>leei</i> Cope	<i>leei</i>
1892 <i>bauri</i> Garman	<i>bauri</i>
1900 <i>variegatus</i> Werner	<i>lepidopygus</i>
1900 <i>baessleri</i> Werner	<i>reissi</i>
1903 <i>gilberti</i> Heller	<i>gilberti</i>
1907 <i>heterurus</i> Werner	<i>heterurus</i>
1910 <i>mentalis</i> Werner	<i>xanti</i>
1910 <i>guayaquilensis</i> Werner	<i>reissi</i>
1910 <i>lobensis</i> Werner	<i>microphyllus</i>
1912 <i>abrupteseriatus</i> Werner	<i>reissi</i>
1912 <i>barringtonensis</i> Van Denburgh	<i>barringtonensis</i>
1924 <i>magister</i> Noble	<i>reissi</i>
1935 <i>mulleri</i> Parker	<i>ventralis</i>
1935 <i>homolepidurus</i> Smith	<i>homolepidurus</i>
1935 <i>lanei</i> Smith	<i>lanei</i>
1936 <i>delcampi</i> Mosauer	<i>delcampi</i>
1940 <i>magnatuberculatus</i> Taylor	<i>lanei</i>

1940 <i>muralis</i> Taylor	<i>muralis</i>
1940 <i>rutteni</i> Hummelinck	<i>rutteni</i>
1942 <i>darwini</i> Taylor	<i>darwini</i>
1942 <i>bordai</i> Taylor	<i>bordai</i>
1942 <i>magnus</i> Taylor	<i>tuberculosis</i>
1952 <i>eduardofischeri</i> Mertens	<i>tuberculosis</i>
1955 <i>wirshingi</i> Kerster & Smith	<i>wirshingi</i>
1960 <i>duellmani</i> Dixon	<i>duellmani</i>
1960 <i>paucituberculatus</i> Dixon	<i>paucituberculatus</i>
1960 <i>insularis</i> Dixon	<i>insularis</i>
1962 <i>underwoodi</i> Dixon	<i>ventralis</i>
1964 <i>davisi</i> Dixon	<i>davisi</i>
1966 <i>angelensis</i> Dixon	<i>angelensis</i>
1966 <i>partidus</i> Dixon	<i>partidus</i>
1966 <i>tinklei</i> Dixon	<i>tinklei</i>
1966 <i>bugastrolepis</i> Dixon	<i>bugastrolepis</i>
1966 <i>santacruzensis</i> Dixon	<i>santacruzensis</i>
1966 <i>apricus</i> Dixon	<i>apricus</i>
1968 <i>palmeus</i> Dixon	<i>palmeus</i>
1968 <i>dixonii</i> Rivero-Blanco & Lancini	<i>dixonii</i>
1970 <i>kofordi</i> new species	<i>kofordi</i>
1970 <i>interandinus</i> new species	<i>interandinus</i>
1970 <i>johnwrighti</i> new species	<i>johnwrighti</i>
1970 <i>angustidigitus</i> new species	<i>angustidigitus</i>
1970 <i>clinatus</i> new species	<i>clinatus</i>
1970 <i>sentosus</i> new species	<i>sentosus</i>
1970 <i>pumilus</i> new species	<i>pumilus</i>

MATERIALS AND METHODS

Approximately 1,800 specimens of *Phyllodactylus* were examined from mainland South America. The material is housed in the American Museum of Natural History (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); Berlin Museum (BM); British Museum (Natural History) (BMNH); California Academy of Science (CAS); Escuela Politecnica Nacional, Quayaquil (EPN); Field Museum of Natural History (FMNH); Hamburg Museum (HM); Los Angeles County Museum of Natural History (LACM); Museo de Ciencias Naturales, Caracas (MCNC); Museo de Biología de la Universidad Central de Venezuela (MBUCV); Museum of Comparative Zoology (MCZ); Museo "Javier Prado," Peru (MJP); Museum of Vertebrate Zoology (MVZ); Neuchatel Museum, Switzerland (NM); San Diego Society of Natural History (SDSNH); Senckenberg Museum, Frankfurt am Main (SMFM); Texas Cooperative Wildlife Collection (TCWC); University of Illinois Museum of Natural History (UIMNH); University of Michigan Museum of Zoology (UMMZ); United States National Museum (USNM); private collections of Charles M. Fugler (CMF), and Raymond B. Huey (RBH).

Descriptions of habitat, behavior, ecology, and color notes of living specimens were obtained in the field by Huey during July, August, and September, 1967 and 1968 and by Dixon and Wright during November and December, 1968. Climatological data were obtained from Robinson (1964) and details of the vegetation were obtained from Macbride (1936). Measurements and analysis of squamation were made by methods described by Dixon (1964b). Sex was determined by the presence of cloacal bones and enlarged postanal tubercles in males, or by dissection.

When we present a description of a species, it will describe all individuals except those covered in the sections on variation.

GENERAL DESCRIPTION OF THE HABITAT OF WESTERN SOUTH AMERICA

The Andes of western South America divide the coastal countries of Ecuador and Peru into three relatively distinct geographic and biological units: the narrow Pacific coast, the Andes and associated valleys, and the tropical forests of the east. Species of *Phyllodactylus* and other lizard genera such as *Tropidurus*, *Dicrodon*, and *Callopiastes* are restricted primarily to the arid coast of western South America and to the northwestern interandean basins of Peru.

The coastal zone, buttressed by the moist Chocohan forests in northern Ecuador (Peters J., 1960), passes south from the thorn scrub and mangrove forests of Ecuador to the barren deserts of Peru and northern Chile. With the exception of a few low passes in northern Peru the Andes to the east form a high barrier generally more than 4,250 meters in areas relevant to discussion.

The deciduous thorn scrub forests extend from the Pacific coast and Andean foothills of Ecuador to the extreme northwestern corner of Peru in the Department of Tumbes, east to the base and foothills of the Andes in the Department of Piura, and then south along the foothills of the Andes into the Department of Lambayeque. Some of the dominant plants of this region include species of *Loxopterygium*, *Caesalpinia*, *Bursura*, *Bombax*, *Capparis*, *Mimosa*, and *Cereus* (Weberbauer, 1936).

The junction of the Ecuadorian thorn scrub and the Peruvian deserts in Tumbes is very narrow and has been attributed to the climatic changes associated with the boundary between the cold waters of the Humboldt Current and the warmer Equatorial Counter Current (Dawson, 1963). The coast of Peru below Tumbes to northern Chile is a barren, arid desert. This desert is not induced by excessively high temperature regimes; rather, it is apparently the result of the aridity associated with the cold Humboldt Current and a rainshadow produced by the Andes (Dawson, 1963; Kendrew, 1961; Murphy, 1948). Rainfall is very low and sporadic throughout much of the area. Most of the water available to plants comes from rivers penetrating the coast from the western slopes of the Andes, high water tables in the Quebradas, and fault zones of northern Peru and fog.

Weberbauer (1936) recognizes two major plant zones in the Peru and Chile deserts. The first runs from Tumbes to a latitude of about 8° south. This area is essentially rainless, except for stormy El Niño years, and extremely barren. Encompassed are such areas as the Sechura Desert in the Department of Piura. Plants tend to be widely scattered and grow as shrubs rather than trees. The substratum is sandy throughout much of the region with a few rocky cerros and the rocky, hard soils of the Quebrada zones. Characteristic features are shifting barchan dunes intermingled with large hummock-like dunes stabilized by *Capparis scabrida* (Koford, 1968). Major plants inhabiting this region include species of *Cryptocarpus*, *Prosopis*, *Capparis*, and *Acacia* (Weberbauer, 1936).

The second zone follows the narrow coast to northern Chile and contains the famous Lomas and *Tillandsia* plant formations. The Lomas are chiefly seasonal carpets of herbs and occasional low trees in areas where the coastal foothills of the Andes rise to heights sufficient to intercept the winter and spring clouds. The increased elevation and lowered temperatures produce considerable condensation in the form of mists making the existence of vegetation possible in an otherwise arid climate. The average annual precipitation recorded in the open is 201 mm for 29 years at Lomas de Lachay in the Department of Ancash (elevation 450 m) compared with only 46 mm for 18 years at nearby Lima (Holdridge, 1964). Major Lomas plants include species of *Aniantum*, *Bowlesia*, *Astrephia*, *Sicyos*, and abundant lichens, mosses and ferns (Weberbauer, 1936).

Unlike the Lomas, the *Tillandsia* association is not dependent on seasonal changes and appears to survive upon atmospheric moisture. *Tillandsia* is most often found on the leeward side and at a lower elevation of hills covered with Lomas vegetation, in drier valleys inland from the coast, and along the coastal plain where no other plants survive. There are large expanses of the deserts where even *Tillandsia* is not found and one is confronted only with barren sand reaching from the Pacific tides to several thousand feet up the Andean foothills.

The deserts of northern Chile extend south to a latitude of about 27°. Extremely barren and arid, much of these deserts are colonized only by *Tillandsia*. South of 27°, the desert is bordered by brush and savanna (Mann 1960). To the east the height of the Andes has apparently prevented invasion by species of *Phyllodactylus* into the *Larrea* deserts of western Argentina.

The northern interandean basins, lying between latitudes 4° to 6° south and longitudes 78° to 80° west (Weberbauer, 1936), are loosely connected with the Peruvian coast by the relatively low passes in the Department of Piura (e.g. Porculla Pass at 2,160 m). These low passes have served as an invasion route for species of *Phyllodactylus* and other species of coastal lizards into a portion of the Amazon drainage.

Surrounded by the higher Andean passes to the north and south and by the Amazonian forests to the east, the interandean basins are limited in extent

and similar in appearance to the coastal foothills of northwestern Peru. The general aridity of these basins, less pronounced than the coast, apparently results from a rain-shadow produced by the eastern chain of the Andes cutting the basins off from the Amazonian moisture.

The interandean basins vary considerably in species composition and physiognomy but are somewhat uniform in vegetative cover with cacti and deciduous plants covering the basin floors except along water courses. The higher slopes are generally matted with dense growths of woody plants (Weberbauer, 1936).

Further details of the habitat of Ecuador, Peru, and Chile can be obtained from Weberbauer (1936), MacBride (1936), Tosi (1960), Koepcke, M. (1954), Koepcke, H. (1961), Dawson (1963), Murphy (1948), Mann (1960), Robinson (1964), Kendrew (1961), Donoso-Barros (1966), and Verdoorn (1945).

Details of the arid and semiarid habitats of Colombia and Venezuela may be obtained from Ruthven (1922) and Shelford (1926).

KEY

The following key is based upon approximately 2,000 specimens of 15 species of *Phyllodactylus* from mainland South America.

The size, shape, and number of scales in the median row beneath the tail is variable within some species but it is generally consistent if a careful examination of the entire, original tail is made. Regenerated tails do not have tubercular scales even if they were present on the original tail. In some instances, the width of the scales of the median row beneath the regenerated tail may be about the same size as those of the original tail.

KEY TO THE SPECIES OF *PHYLLODACTYLUS* OF MAINLAND SOUTH AMERICA

- 1a. Preanal scale single, greatly enlarged, 10-20 times larger than belly scales 2
- 1b. Preanal scales small, equal in size to other belly scales 4
- 2a. Tail smooth, without enlarged rows of lateral tubercles 3
- 2b. Tail keeled, with four rows of lateral tubercles (northern Chile) *heterurus*
- 3a. Digits short, fourth toe lamellae 12-15 (13.1), terminal lamellae large (southern Peru to northern Chile) *gerrhopygus*
- 3b. Digits long, fourth toe lamellae 15-20 (16.8), terminal lamellae very small (coastal south central Peru) *angustidigitus*
- 4a. Dorsal tubercles small, rounded, sometimes slightly keeled, not arranged in regular rows; ventral surface of tail with all scales of equal size . . . 5
- 4b. Dorsal tubercles large, trihedral, arranged in regular rows; ventral surface of tail with or without enlarged scales in median row 6
- 5a. Terminal lamellae of digits much enlarged, most of claw hidden when viewed from above; nostril not swollen (extreme northwestern Peru and probably southwestern Ecuador) *inaequalis*

- 5b. Terminal lamellae of digits very small, most of claw exposed when viewed from above; nostril greatly swollen (central to extreme north-western Peru) *microphyllus*
- 6a. Dorsal surface of tibia without enlarged tubercles 7
- 6b. Dorsal surface of tibia with enlarged tubercles 9
- 7a. Dorsal surface of tibia with very small granular scales; ventral surface of tail with all scales of median row enlarged, rectangular (northwestern Peru) *clinatus*
- 7b. Dorsal surface of tibia with round, elevated scales; ventral surface of tail with or without some enlarged, rounded scales in median row . . . 8
- 8a. Tubercles in paravertebral row from head to base of tail 44-53; no scales on ventral surface of tail enlarged (coastal foothills of central Peru) *lepidopygus*
- 8b. Tubercles in paravertebral row from head to base of tail 65-81; some scales in median row of ventral surface of tail enlarged, rounded (Maranon Basin, northwestern Peru) *interandinus*
- 9a. Tubercles present on dorsal surface of forearm 10
- 9b. Tubercles absent on dorsal surface of forearm 13
- 10a. Terminal lamellae of digits much enlarged; claw mostly hidden when viewed from above; ventral surface of tail with all scales of median row enlarged, rectangular 11
- 10b. Terminal lamellae of digits small, narrow; claw mostly exposed when viewed from above; ventral surface of tail with a few scales of median row enlarged, rounded (Lima, Peru) *sentosus*
- 11a. Large species, average snout-vent length of 64 mm; 19-26 paravertebral tubercles between axilla and groin 12
- 11b. Small species, average snout-vent length of 38 mm; 16-21 paravertebral tubercles between axilla and groin; (northwestern Peru and probably southwestern Ecuador) *kofordi*
- 12a. Distal one-third of tail with at least two or more rows of tubercles; scales across venter 18-24; (northern Venezuela and Colombia) . . . *ventralis*
- 12b. Distal one-third of tail without tubercles; scales across venter 26-28; (central Venezuela) *dixoni*
- 13a. Scales of supraocular region largest of interorbital scales; enlarged tubercles usually present on dorsal surface of thigh; maximum snout-vent length 51 mm 14
- 13b. Scales of supraocular region smallest of interorbital scales; enlarged tubercles usually absent on dorsal surface of thigh; maximum snout-vent length 75 mm (northwestern Peru and west central Ecuador) . . . *reissi*
- 14a. Scales on proximal one-fourth of tail homogeneous; internasals usually separated along median edges (Huancabamba Basin, northwestern Peru) *johnwrighti*
- 14b. Scales on proximal one-fourth of tail heterogeneous; internasals usually in contact along median edges (west central Ecuador) *pumilus*

SPECIES ACCOUNTS

Phyllodactylus heterurus Werner

Phyllodactylus heterurus Werner 1907. Ann. Univ. Chile, 121:149.

Holotype. Adult male, (lost in a fire), collected by C. Reiche 1902. Type-locality. Oasis de Pica (Desierto de Tarapaca), Department of Tarapaca, Chile.

Definition and Diagnosis. This species is known only from the holotype that was destroyed by a fire. *Phyllodactylus heterurus* is a small gecko with a maximum snout-vent length of 38 mm; dorsal surfaces of head and body smooth, without tubercles; tail with four rows of tubercles, two on each lateral surface; preanal plate present; terminal lamellae of digits moderately large.

This species is distinguished from all other species of *Phyllodactylus* except *gerrhopygus* and *angustidigitus*, by the presence of an enlarged preanal plate; from *gerrhopygus* and *angustidigitus* by the presence of four rows of tail tubercles, with anteriorly projecting tips.

Description of holotype. Since the holotype is no longer extant, we submit a translated version of Werner's (1907) original description: Head ovoid, very much longer than wide; snout longer than the distance from the posterior corner of eye to ear and two times the length of eye; frontal region not concave; ear opening small, horizontal and elliptical; body decidedly thin; inferior aspect of digits similar on anterior and posterior limbs, with wide plates whose distal ends are visibly wider than their proximal portion; dorsal aspect of body with small scales that are ovoid, smooth, somewhat convex; rostral scales pentagonal, somewhat concave posteriorly, with a groove beginning on posterior border; nasal opening surrounded by rostral, supralabial and three nasals; nine supralabials and seven infralabials; nasal (internasals) scales separated on median line by an azygous scale; mental two times longer than wide with posterior border rounded, lateral sides parallel; chin without enlarged scales (postmentals absent); scales in gular region very small; ventral scales small, smooth, circular and overlapping; tail cylindrical, with transverse series of robust, conical tubercles whose points are directed anteriorly.

Color and pattern on dorsum lead gray with black irregular spots and lines; lines unite on dorsal side to form transverse bands with obscure outlines; tubercles on tail brick red.

Total length 71 mm, head 12 mm in length by 7.5 mm in width; tail 30 mm in length.

Comments. Donoso-Barros (1947) redefined the holotype prior to its destruction and further distinguished the species from *gerrhopygus* by its large, round eye, ovoid head with sharply pointed snout, and gave preservation colors that differed from those given by Werner (1907).

As far as we can determine, no additional specimens have been taken since 1902, therefore data are not available on its habits, habitat, or natural history.

Distribution. Known only from the type locality (fig. 5).

***Phyllodactylus gerrhopygus* (Wiegmann)**

Diplodactylus gerrhopygus Wiegmann 1835. *Nova Acta Leop.-Carol.*, 14:242.

Phyllodactylus gymnopygus Dumeril and Bibron 1836. *Erp. Gen.*, 3:394.

Phyllodactylus gerrhopygus, Boulenger 1885. *Cat. Liz. Brit. Mus.*, 1:95.

Phyllodactylus inaequalis, (part) Burt & Burt, 1931. *Bull. Amer. Mus. Nat. Hist.*, 61(7):250.

Holotype. Lost, formerly in Berlin Museum, collector and date of collection unknown. Type-locality. Chile.

Definition. An average size gecko with a maximum known snout-vent length of 56 mm; large preanal plate present; dorsal tubercles absent; tibia and femur tubercles absent; ear denticulate on anterior and posterior margins; median row of scales beneath tail equal in size to other ventral scales; tail about 50 percent of total length; mental much longer than wide and postmentals absent; terminal lamellae of digits large, longer than wide; claws of digits large, usually extending slightly beyond tip of terminal lamellae; dorsal markings present or absent, if present, consisting of broad bands or blotches; tail usually banded (fig. 8a).

Diagnosis. This species may be distinguished from all other species, except *angustidigitus* and *heterurus*, by the presence of an enlarged preanal plate; from *heterurus* by the absence of enlarged lateral tubercles on the tail; from *angustidigitus* by the larger toe pads and shorter digits.

Description. Rostral about as high as wide, its dorsal edge "M" shaped, with a short median vertical groove; two internasals, somewhat triangular in shape, their median edges not in contact but separated by three azygous scales (snout granules); internasals bordered posteriorly and medially by small granules and postnasal of each side; nostril surrounded by rostral, labial, internasal, and two postnasals; nostril area somewhat swollen by elevation of postnasals and internasal; first supralabial in broad contact with ventral edge of nostril; moderate depression between internasals, slight depression in frontal region; scales in posterior loreal region about twice the size of midorbital scales; eye large, its diameter contained in snout length about 1.5 times; eyelid with two rows of granules and one larger outer row of scales, the last three to six are pointed; diameter of ear contained in eye diameter about 2 times; ear opening denticulate on anterior and posterior margins, rear of head granular; usually 8 supralabials and 5 or 6 infralabials to point below center of eye; mental straight-edged, rounded posteriorly, about 2.5 times longer than wide; postmentals absent, mental bordered by small chin scales.

Dorsum without enlarged tubercular rows, scales subequal in size, somewhat flattened, about half size of midventral scales; latero-ventral scales smaller than dorsal and ventral scales; very large preanal plate (scaleless), surrounded by about 25 ventral scales; preanal plate about 20 to 30 times larger than adjoining ventral scales; enlarged postanal scales on each side, somewhat flattened.

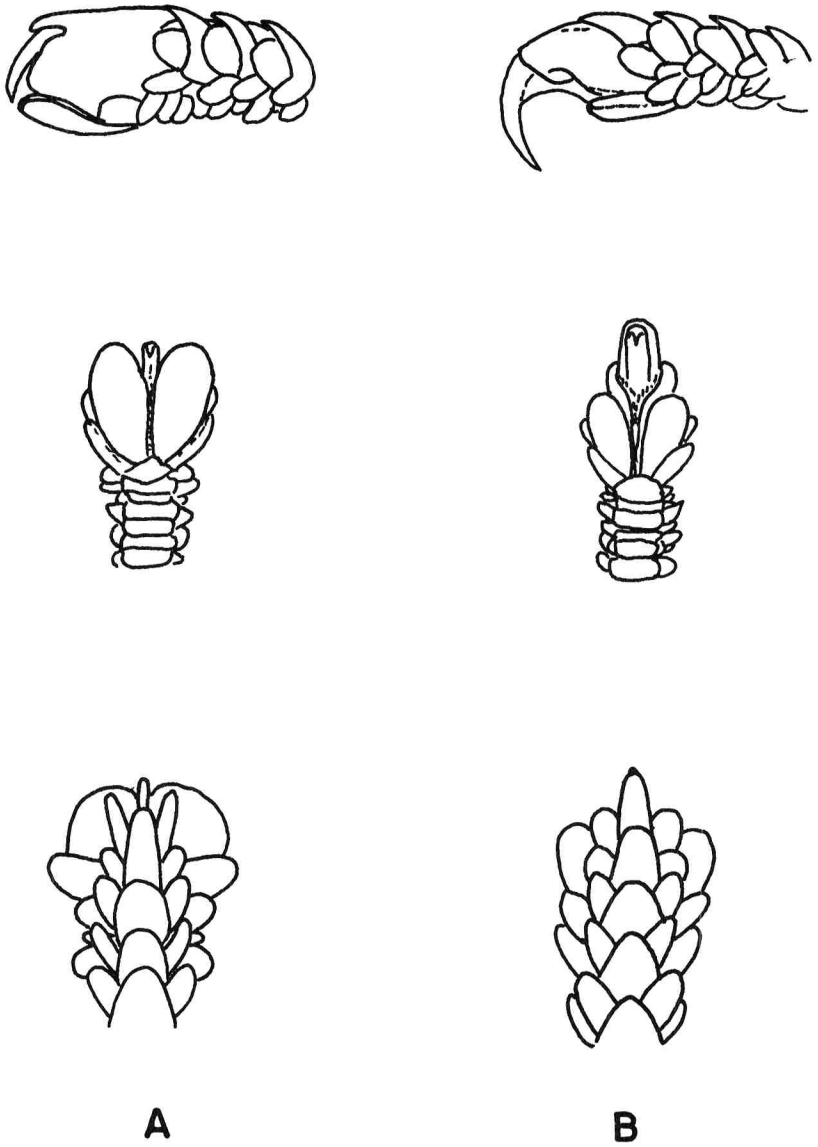


Figure 1. Lateral, ventral and dorsal view of the distal end of the fourth toe of (A) *P. gerrhopygus* and (B) *P. angustidigitus*.

Dorsal surface of upper arm with flattened scales, forearm with larger, slightly elevated scales; dorsal surface of thigh and lower leg with flattened, but slightly elevated scales; claw moderately exposed when viewed from below; terminal lamellae twice as long as wide, somewhat reduced in size with claw extending beyond tip of terminal lamellae; tail with all scales of ventral surface of equal size, scales of dorsal surface smaller than those of ventral surface.

Color in alcohol: ground color tan, with light orange tint; dorsum with four broad light brown bands with undulating edges bands composed of suffusion of brown and tan scales intermixed (freckled), with tan interspaces slightly wider than dark bands; upper and lower arms and legs with faint brownish bands; tail with nine bands similar in color to dorsal bands, with yellowish tan interspaces; posterior part of head and nape with reticulating brown lines on ground color; top of head spotted with brown; brownish stripe from nostril to eye; brownish reticulating lines between eye and ear; labials faintly flecked with dark brown; ventral surfaces of head, body, and tail immaculate white.

Variation. Snout-vent length of young adult and adult males varies from 32 to 56 mm (43.9), females from 32 to 55 mm (42.8), juveniles from 25 to 31 mm (28.9), and males and females together average 42.7 mm; postmentals absent in 96.4 percent of sample; three of 98 specimens have two postmentals, one specimen had one postmental on one side, none on the other side; mental much longer than wide, extending posteriorly beyond the tips of adjoining labials; number of transverse chin scales immediately following and touching mental vary from 3 to 8 (4.6); scales across midorbital region vary from 13 to 20 (15.9), across the snout at level of third labial from 12 to 18 (14.7); number of scales bordering internasals vary from 6 to 10 (7.7), internasals always separated along median line by 1 to 3 granules; transverse row of scales across venter vary from 20 to 30 (24.7), longitudinally 64 to 76 (69.1); preanal shield large, without scales, generally 20 to 30 times larger than adjoining scales; scales between eye and nostril vary from 8 to 12 (10.4); number of lamellae beneath fourth toe vary from 12 to 15 (13.1); all scales of dorsum, limbs, and tail subequal in size, relatively smooth, and slightly elevated to some extent; supralabials vary from 7 to 9 to a point below center of eye, 8 being most common; dorsal bands (if present) number 4 to 6, tail bands 6 to 9.

Color pattern consists of body bands or blotches that tend to appear freckled with tan and brown scales intermixed, but occasionally some specimens are uniform tan or light brown; tail usually banded; belly usually immaculate white; parietal region and lateral area of head behind ear usually with reticulated brown lines on ground color; limbs usually faintly banded with brown.

Habitat and natural history. Of 98 individuals examined, only five were collected by one of us. One of these was collected during the day from beneath

a piece of tin in an open sand dune area where some vegetative cover was present. Four individuals were found active after dark along the base of sand dunes approximately 150 m from a sand and rock rubble beach, and approximately 50 m from a ravine where some plant cover was present. The dunes were approximately 50 to 75 m in height and without vegetation. Silverfish, beetles, and spiders appear to be the only food items available in the area where the five specimens were taken.

The absence of individuals along the beach might be explained by the presence of hundreds of ghost crabs occupying the intertidal zone.

One specimen in the University of California Museum of Vertebrate Zoology with field data was taken from beneath a stone in a sandy wash. Garman (1875) mentions that his specimens were found beneath stones in a sandy plain near Arequipa, Peru.

Through the courtesy of Stanley W. Taft, a Peace Corps Volunteer from New Mexico State University, we were able to obtain some habitat data on *P. gerrhopygus* from the San Juan de Marcona area of Peru. The San Juan Marcona area is approximately 157 airline km SSE of Ica, at an elevation of 0 to 150 m. The general terrain is rolling sand hills with sandy beaches and large outcroppings of a red limestone-like formation. Taft (*personal communication*) indicated that large hematite deposits were present in the area which probably give the red color to the sandy areas. The only vegetation of the immediate area consisted of a few scattered *Capparis sp.* shrubs.

A series of *P. gerrhopygus* collected by Taft were taken from rock walled terraces, outside walls of houses, and from sidewalks. Taft indicated that the geckos were occupying small holes made by the absence of plaster or mortar between the rocks and cement blocks of terrace walls and houses. All of his specimens were collected at night, and two were taken from a terrace wall near a sodium vapor light. Taft stated that several were seen along the sandy beaches at night but were not collected.

From an examination of living and preserved females, there appears to be only one egg laid per clutch. Nests of this species have not been found under natural conditions.

Distribution. This gecko apparently occupies a variety of habitats along the desert coast, foothills, and mountains from central Peru to northern Chile between the elevations of sea level and 2,750 m (fig. 2). We have examined 98 specimens from the following localities: CHILE. *Tarapaca*: Arica UMMZ 11576; 3 mi S Arica AMNH 65343-59. 50 km from Iquique MCZ 56247. Pica FMNH 6327-29, 9984. Pintados FMNH 6326. Putre FMNH 6330, 6331(3), 6332-41. PERU. *Arequipa*: Arequipa AMNH 22238, 36525-26, FMNH 3577(4), 43769. 12 mi SE Camana CAS 84769. Chucarapi FMNH 34236-37. 16 km S. La Joya MVZ 84636. Mollendo CAS 84760-68, FMNH 34248(4). Tambo FMNH 4005-06. Vitor FMNH 34179. Yura FMNH 34047(9), 34205(5), 34182-83, 34190. *Ica*: 1 km NNW Jaguay LACM 48465-66, TCWC 28064-65; Marcona TCWC 27874-78. 6.3 km ESE Pozo

Santo TCWC 28063. San Juan Port (Salamanquejo) SDSNH 31091-92.
 Lima: Isla San Lorenzo USNM 17542 (probably in error).

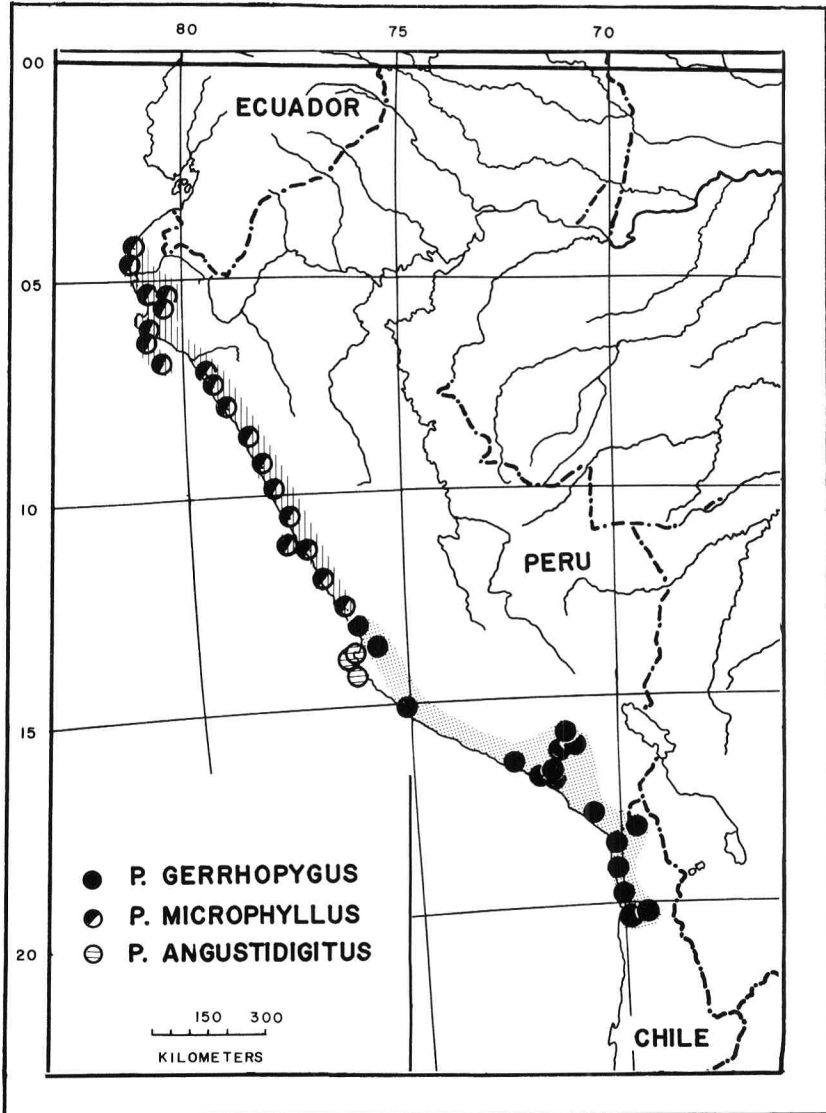


Figure 2. Distribution of *P. gerrhopygus*, *P. microphyllus* and *P. angustidigitus* in western South America.

***Phyllodactylus angustidigitus* sp. nov.**

Phyllodactylus gerrhopygus, (part) Burt and Burt 1930; Proc. U. S. Nat. Mus., 78(2849):4.

Holotype. Adult male, TCWC 27915, collected by James R. Dixon and John W. Wright, 11 November 1968. Type locality. One km S new port of Pisco, northeast side of Paracas Peninsula, 19 km by road south and west of Paracas, Department of Ica, Peru, sea level.

Definition. A moderate-sized gecko, maximum known snout-vent length of 57 mm; large preanal plate present; scales of head, body, tail, and limbs uniform in size; tubercles absent; no enlarged scales beneath tail; tail 48 to 52 percent of total length; mental much longer than wide, without enlarged postmentals; terminal lamellae very small, claw greatly extended beyond tip of terminal lamellae; fourth toe lamellae numerous (15 to 20) (fig. 8a, 8b).

Diagnosis. *Phyllodactylus angustidigitus* differs from all other species of *Phyllodactylus* except *gerrhopygus* and *heterurus*, by having an enlarged preanal plate; from *heterurus* by absence of tail tubercles and small terminal lamellae; from *gerrhopygus* by small terminal lamellae and high number of fourth toe lamellae, 15 to 20, rather than 12 to 15.

Description of holotype. Rostral about twice as wide as high, its dorsal edge with a broad "M" shape, with dorsal vertical groove one-half depth of rostral; two internasals, somewhat rounded, their median edges separated by two granules, bordered posteriorly by two granules and postnasal of each side; nostril surrounded by rostral, labial, internasal, and two postnasals; first labial in narrow contact with ventral edge of nostril; shallow depression between internasals, no depression in frontal region; 10 scales on line between nostril and eye; scales in posterior loreal region about twice size of midorbital scales; 15 scales across snout at level of third labial, 14 scales at anterior edge of orbits, 18 midorbital scales; eye large, its diameter contained in snout length 1.7 times; eyelid (brille) with one row of granules and one larger outer row of scales, last three to four are pointed; diameter of ear contained in diameter of eye 2.3 times; ear opening denticulate on posterior margin; all dorsal scales small, smooth, slightly convex; seven supralabials and six infralabials to point below center of eye; mental with parallel sides, about 2.5 times longer than wide, bordered posteriorly by six chin scales; enlarged postmentals absent; dorsum with 75 granules and scales around body; venter with 29 scales across belly, from throat to vent 79; postanal tubercles number four on one side, three on opposite side; dorsal surfaces of limbs similar to dorsum; lamellae formula for hand 7-11-12-13-11, foot 7-12-16-18-16; claw completely visible when viewed from below; terminal lamellae very small, not much wider than width of fifth lamella counted from base of digit.

Measurements in mm; snout-vent length 53.5, axilla-groin length 25.8, length of leg 24.0, length of arm 18.0, length of tail 55.0, length of head 13.3, depth of head 6.2, width of head 10.5, length of snout 5.0, diameter of eye 2.9, diameter of ear 1.2, distance from eye to ear 3.8.

Color in life: ground color yellowish tan; dorsum with fine network of thin, dark brown, reticulating lines, broken at midbody by median stripe of ground color, bordered on each side by dark brown line; paravertebral lines begin at shoulder and terminate at level of groin; arm with four light brown bands with interspaces of ground color; lower part of leg with three indistinct light brown bands; upper part of thigh with faint indication of bands with irregular edges; tail with 11 broad, brownish black bands that contain light brown diffuse spots within their borders, interspaces ground color, about one-third width of dark bands; head with fine network of light brown, reticulating lines; diffuse brownish black stripe from nostril to eye; iris of eye blue gray with black and silver flecks; ventral surfaces dirty white, with grayish wash across chest and throat.

Variation. Snout-vent lengths of young adult and adult males vary from 41 to 57 mm (50.3), females from 37 to 54 mm (47.8), juveniles from 30 to 36 mm (32.8), and males plus females average 48.7 mm; postmentals absent in 99.3 per cent of sample, two of 254 individuals had three enlarged postmentals; number of chin scales immediately following and touching mental vary from 3 to 8 (5.8); scales across snout at level of third labial vary from 13 to 17 (15.1), across midorbital region 16 to 20 (18.2); internasals separated by small granules in 99.5 per cent of sample; scales bordering internasals vary from 7 to 10 (8.7); scales across venter vary from 23 to 28 (25.6), from throat to vent 64 to 70 (67.5); enlarged preanal shield without scale covering, 20 to 25 times larger than surrounded scales; scales between eye and nostril vary from 10 to 12 (11.0); number of fourth toe lamellae vary from 15 to 20 (16.8).

Ventral color generally uniform dirty white with some grayish wash on chest and throat; dorsal coloration highly variable, from almost uniform wash of yellowish tan to broad, dark brown bands; majority of individuals with some form of dark dorsal reticulations or bands, usually heavily suffused with ground color; tail generally banded, but width of dark bands and light interspaces highly variable; regenerated tails either near black with light areas or ground color with dark flecks; ground color variable, from light tan to very dark grayish brown.

Comment. Since populations of *angustidigitus* appear to be closely related to *gerrhopygus*, the following statement of our ideas on the evolutionary trends in this population emphasizes its rate of speciation. The Paracas Peninsula was apparently an island, probably as late as the Pleistocene, and within recent times has become connected to the mainland. The attributes of *angustidigitus* populations on Islas Sangallan and Viejas are identical with those of the Paracas Peninsula, lending some support to this idea. The original invasion of the islands by prototypes of a *angustidigitus*-like population may have occurred by rafting, or by land invasion while the land masses were connected early in the formation of the continental shelf.

The islands and peninsula populations are presently restricted in distribu-

tion to the narrow shell and rubble beaches probably due to cover and food availability. The adaptations for living in the shell and rubble resulted in the reduction of the size of the terminal lamellae and increase in the exposure of the claw as a means of walking and digging in this environment. The longer toe length affords better traction on a shell and rubble substratum. The large terminal lamellae adapted to sand or a scansorial habit are unsuited for life on a shell or rubble beach.

The presence of a few *angustidigitus* living along a mud beach towards the southeast part of the peninsula where it connects with the mainland and also two individuals found in beach dunes on the mainland a few kilometers away may indicate a recent invasion of the mainland by this species. This may be due, in part, to the great density of the population now occupying the shell and rubble beaches. Density dependent factors related to population pressure may be forcing individuals farther away from their preferred habitat. Hence, a few hardy individuals are surviving in a marginal habitat which is generally unfit for the population as a whole.

An individual of *P. gerrhopygus* was found 25 kilometers from the easternmost record of *P. angustidigitus*, with no indication of intergradation or hybridization between the two species. Thus some period of genetic isolation of the peninsular population has allowed *angustidigitus* to evolve through natural selection.

Habitat and natural history. This species is apparently restricted to the narrow shell and rubble beaches of the Paracas Peninsula and its associated islands. Of 241 specimens taken from the east side of the peninsula only three were found more than 10 m from the storm tide zone. One was found beneath a stone at the edge of a bluff approximately 20 m from the ocean and two were found about the same distance away on a small granite hill covered with a thin layer of sand. There are no macroscopic plants on the peninsula and no surface water. Away from the beach the only physical cover consists of a few outcrops of granite and small amounts of condensed salt forming a hard surface crust. The only food items available appear to be silverfish, amphipods, and spiders that live in beach debris of the storm and intertidal zones. The paucity of food and cover elsewhere on the peninsula may account for the concentration of individuals along the storm and intertidal zones. A total of 157 individuals were taken along a 100 m stretch of shell beach in one evening between the hours of 8:00 and 9:30 p.m.

Individuals of this species emerge from cover soon after dark, but they seem to be most abundant two to three hours following darkness. Several individuals were observed emerging from beneath dried seaweed and shell debris about 9 p.m. During the day individuals were found beneath the carcasses of dead birds, dried seaweed, and assorted trash cover. Seven specimens were found along a narrow mud beach where the only retreat consisted of cracks in a vertical mudstone cliff. All specimens were found in cracks one

to two meters above the mud beach. The only food items observed were a few amphipods under damp seaweed on the beach and pseudoscorpions in cracks along the mudstone cliff.

Wherever the beach was composed principally of sand, only a few individuals of this species could be found. These were taken along the base of cliffs bordering the beach even though there was considerable storm debris near the beach. The near absence of geckos along these stretches of beach may be due to the great abundance of ghost crabs occupying the storm and intertidal zones of these areas. Crabs were not observed feeding on geckos but their nocturnal activity corresponded with that of the geckos, and the crabs may have been possible predators.

When disturbed, the majority of geckos attempted to escape by running towards the cliffs above the beach or hiding beneath shell debris. However, on two occasions individuals ran into the ocean. One immediately turned and made its way back to shore while the other swam a few meters out to sea. The latter individual, apparently tired, spread its limbs horizontal to the body and allowed wave action to return it to shore.

A few individuals were observed climbing boulders and cliffs during their nocturnal activities. Their actions were slow and deliberate and when disturbed, frequently fell off the surface in an attempt to escape. They seem to have difficulty in clinging to vertical surfaces and any rapid movement on their part dislodges their hold on the surface. The absence of large terminal lamellae normally found in scansorial species is a probable factor in their inability to move rapidly on vertical surfaces.

Body temperatures were taken from several individuals during their nocturnal activities and found to be closely associated with the substratum temperature, varying approximately 0.5°C above or below the latter temperature.

This species appears to lay only one egg at a time. All gravid females examined contained one large developing egg and those confined in captivity laid only one egg.

Distribution. This species is apparently confined to the narrow shell and rubble beaches of the Paracas Peninsula and associated islands of Peru although a few individuals may be found on the periphery of the former area (fig. 2).

Specimens (246) have been examined from: *Ica*: Islas Sangallan USNM 38570; Islas Viejas SDSNH 31093-94; Lagunillas (Gallinazo) Bay FMNH 34337-40; Paracas Peninsula AMNH 36505-07, 36510-12; 7.2 km SW Paracas LACM 48705, TCWC 27983; 1 km S Puerto Pisco (new) LACM 48593-627, TCWC 27915, 27944-79; 3 km S Puerto Pisco (new) LACM 48632-704, 48706, TCWC 27984-8062; 7 km S Puerto Pisco (new) LACM 48628-31, TCWC 27980-82.

Phyllodactylus inaequalis Cope

Phyllodactylus inaequalis Cope 1876. Jour. Acad. Nat. Sci., Phila., ser. 2, 8:174.

Holotype. Adult female, ANSP 11365, collected by James Orton in 1867-1868. Type-locality, from Pacasmayo, Department of Lambayeque, Peru.

Definition. A small gecko with a maximum known snout-vent length of 42 mm; tibia and femur tubercles absent; ear denticulation absent; tubercles on rear of head absent; median row of scales below tail equal in size to adjoining scales (occasionally widened in some specimens); enlarged preanal plate absent; enlarged dorsal rows of flattened tubercles usually absent at midbody (occasionally two rows present); tail about 45 per cent of total length; tail tubercles absent; terminal lamellae of digits distinctly widened and truncate; ground color light gray with dark gray bands usually present; tail usually banded with dark gray on light ground color; belly brilliant white to light yellow (fig. 12b).

Diagnosis. *Phyllodactylus inaequalis* may be distinguished from *gerhopygus*, *angustidigitus*, and *heterurus* by the absence of an enlarged preanal plate; from *clinatus*, *dixonii*, *internadinus*, *pumilus*, *johnwrightii*, *kofordi*, *lepidopygus*, *sentosus*, *reissi*, and *ventralis* by having less than 10 dorsal rows of enlarged, flattened tubercles at midbody; from *microphyllus* by its smaller maximum snout-vent length (42 mm rather than 56 mm), and by having the terminal lamellae of the digits distinctly enlarged and truncate with claw mostly hidden rather than very small terminal lamellae with claw mostly exposed.

Description. Rostral twice as wide as high, its dorsal edge almost straight with a short median vertical groove; internasals somewhat rounded, their median edges in narrow contact, bordered posteriorly by small granules and postnasal of each side; nostril surrounded by rostral, labial, internasal and two postnasals; first supralabial in narrow contact with ventral edge of nostril; shallow depression between internasals, slight depression in frontal region; scales in posterior loreal region about two to three times larger than scales in midorbital region; eye large, its diameter contained in snout length about 1.4 times; eyelid with two rows of granules and one large outer row of scales, last three to five are pointed; diameter of ear contained in eye diameter four times; ear opening small, scales on anterior edge rounded, subequal, those on posterior margin rounded but with elevated scales lying within the ear opening; rear of head granular, without larger intermixed tubercles; six to seven supralabials and five to six infralabials to a point below center of eye; mental bell-shaped, longer than wide, bordered posteriorly by two postmentals; postmentals wider than long, their median edges in narrow contact, followed by transverse row of granular scales.

Distal one-third of dorsum with none to 10 indistinct rows of slightly

enlarged, flattened tubercles, paravertebral row of each side reach to shoulder in some individuals; paravertebral rows usually separated from each other by four rows of granules; each tubercle of enlarged dorsal series separated from preceding tubercle by two to four granules; postanal tubercles number four on each side, distinct and elevated.

Dorsal surface of upper arm with flattened, rounded scales, forearm with slightly smaller scales that are rounded and slightly elevated; dorsal surface of thigh and lower leg with rounded, slightly elevated scales; claw short but visible when viewed from below; terminal pad large, longer than wide with somewhat rounded edges; about every other median scale on ventral surface of tail slightly widened; cloacal sacs with external plicate lips.

Color in alcohol: ground color light gray; dorsum with dark gray transverse bands, somewhat broken along midline of back; width of bands equal to ground color interspaces; dorsal bands somewhat diffuse with white granules intermixed with few black granules; lateral area of body with suffusion of intermixed white, gray, and black granules; arms and legs with suffuse spotting of gray, brownish gray, and black granules and scales, without definite pattern; tail with five dark gray bands, twice as wide as whitish interspaces; top of head with suffusion of dark gray and ground color, no definite pattern; dark gray stripe from nostril through eye, over ear, to just posterior of arm insertion, bordered above and below by pale whitish line from internasal to just posterior of ear; belly brilliant white.

Variation. Snout-vent length of subadult and adult males varies from 33 to 40 mm (37.0), females from 30 to 42 mm (36.8), juveniles from 19 to 28 mm (23.0), males and females together average 36.9 mm; two postmentals in all specimens examined; postmentals contacting first labial in only 54.6 per cent of the sample, first and second labials in 22.7 per cent, and no labials contact in 22.7 per cent; number of transverse scales immediately following the postmentals vary from 7 to 10 (8.3); scales across the midorbital region range from 20 to 22 (20.8), across the snout at level of third labial 20 to 24 (21.3); number of scales bordering internasals vary from 7 to 8 (7.3) with an azygous scale separating the internasals in 3 to 59 specimens; transverse row of scales across belly vary from 26 to 32 (29.4), longitudinally 55 to 62 (58.4); scales on a line between nostril and eye vary from 11 to 12 (11.6); lamellae beneath fourth toe vary from 10 to 12 (10.7); enlarged rows of dorsal tubercles scarcely evident at midbody, none present in seven specimens, two rows present in four specimens; dorsal tubercular rows more evident across rump and base of tail; rows of tubercles across base of tail vary from four to eight, six being most common.

Color pattern fairly consistent, with shades of gray ground color and dark gray bands somewhat variable; bands may be straight or slightly undulating; all have dark grayish brown spot in center of parietal area; dark head stripe from nostril to arm in seven specimens, to anterior third of body in

three, to ear in one; body bands (if present) number 4 to 6, five being most common; tail bands (if present) number 6 to 7 in about equal numbers; tail bands generally fade towards distal fourth of tail.

Comments. (See comments under *Phyllodactylus microphyllus*.)

Habitat and natural history. *Phyllodactylus inaequalis* principally inhabits the desert foothills of northwestern Peru. Specimens have been taken in a variety of foothill localities where the vegetation may be classified as very sparse to dense.

The Cerro Amotape area rises out of the northern end of the Sechura Desert and is contiguous to the northeast foothills of the western chain of the Andes. This area is moderately barren with exfoliating granite boulders and abundant cacti, but the vegetation is less dense than other foothill localities to the east. Three specimens were obtained in a dry wash on the south slope of the cerro where scattered small shrubs were present.

The Las Lomas area lies at the foot of the Andes and contrasts with the Cerro Amotape region in having more dense vegetation, principally thorn scrub with scattered larger trees. One lizard was found foraging on the ground beneath small leafless shrubs.

The Abra de Naupe area lies at the foot of the Andes south and east of the Las Lomas region. This region consists of low hills composed of weathering granite (nonexfoliating) with scattered cacti, mesquite, acacia, and small amounts of grass. One specimen was found during the day beneath a rotting cactus.

The Pacasmayo area (type locality) lies near the base of the Andes where the southern end of the Sechura Desert meets the Jequetepeque River. The vegetation is very sparse, consisting of mesquite groves along the river and a few cacti on the foothill slopes. A few individual plants of *Capparis* sp. occur in sandy flats at the base of the foothills. Seven individuals were taken at dusk from a flat area of hardpan soils at the base of the foothills on the north side of the Jequetepeque River. All seven specimens were found beneath such trash items as cardboard, cement sacks, and tarpaper.

The majority of specimens (47) collected by us were taken in the Cerro de la Vieja region. Although geographically a foothill locality, this cerro is separated from the main foothills lying several kilometers to the north and east. The cerro is approximately 150 m in height, with large exfoliating granite boulders and moderate plant cover. The larger plants of the area are mesquite, palo verde, cacti, and *Capparis* sp. (tree form). During the day *P. inaequalis* were found beneath a bridge under a stone and under small exfoliating flakes of granite on large boulders. Individuals were found actively foraging on the ground or on small boulders at night. Most individuals were found on the ground within one-half meter of the base of boulders. One lizard was taken on open soil approximately five meters from the nearest cover, and one individual was observed climbing a small shrub.

In all regions mentioned above except for the Pacasmayo area, *P. inae-*

qualis is sympatric with *reissi* and *kofordi*. There are however, some microhabitat preferences for daytime retreats unique to each species. Large exfoliating granite flakes were utilized by *P. reissi*, small flakes by *inaequalis*, and small burrows under boulders or cracks in the soil by *kofordi*. After dark, *P. reissi* generally preferred large vertical faces of boulders on which to forage, *P. inaequalis* generally on the ground at the base of boulders, and *P. kofordi* on boulders and on the ground.

The nocturnal body temperatures of *P. inaequalis* usually ranged between the substratum and air temperatures but generally closer to the substratum than to the air temperature. This was found to be true for other species as well.

This species lays only one egg at a time. Captive females laid only one egg and preserved gravid females contained a single egg, either in the right or left oviduct.

Distribution. This species occurs in widely scattered localities in northwestern Peru. It appears to be restricted to the desert foothills bordering the Sechura Desert (fig. 4). Specimens (59) have been examined from the following localities: *Lambayeque*: 7 km S Motupe LACM 48495, 48500-18, TCWC 28308-27, MVZ 82174, 85329-33, 7.2 km W Naupe TCWC 28328. *Libertad*: Pacasmayo ANSP 11365; 16.7 km ENE Pacasmayo LACM 48496-99, TCWC 28305-07. *Piura*: Cerro Amotape MVZ 82170, 82172, 82283; 5 km E Las Lomas MVZ 82171.

***Phyllodactylus microphyllus* Cope**

Phyllodactylus microphyllus Cope 1876. Jour. Acad. Nat. Sci. Phila., ser. 2, 8:175

Phyllodactylus inaequalis, (part) Noble 1924. Occ. Paps. Boston Soc. Nat. Hist., 5:111.

Phyllodactylus gerrhopygus, (part) Burt and Burt 1931; Bull. Amer. Mus. Nat. Hist., 61(7):250.

Holotype. Adult male, ANSP 11364, collected by James Orton in 1868-69. Type locality. Valley of Jequetepeque, Peru (Department of Lambayeque).

Definition. An average-sized gecko with a known maximum snout-vent length of 58 mm; very small terminal lamellae on all digits with fingers and toes short; dorsal tubercular rows indistinct, composed of small flat, oval tubercles that seldom form regular rows; enlarged tubercles absent from head, limbs, and tail; scales of ventral surface of tail uniform in size; scales surrounding nostril greatly swollen; ventral color of body, limbs, and tail brilliant white (fig. 9b).

Diagnosis. This species is readily distinguished from *P. gerrhopygus*, *heterurus*, and *angustidigitus* by the absence of an enlarged preanal plate; from *clinatus*, *dixonii*, *lepidopygus*, *interandinus*, *kofordi*, *sentosus*, *johnwrighti*, *reissi*, *ventralis* and *pumilus* by the absence of enlarged, regular rows of trihedral tubercles on dorsum; from *inaequalis* by the presence of a distinct swollen region about the nostril, larger size, and very small terminal lamellae.

Description. Rostral about twice as wide as high, its outer posterior edges elevated along inner edge of nostril; internasals small, rounded and swollen, their median edges separated in most specimens by three rows of granules; median and posterior borders of internasals contact small granules and postnasal of each side; nostril surrounded by rostral, internasal, and two postnasals, all greatly swollen about nostril; first supralabial not in contact with ventral edge of nostril; shallow depression between internasals and in frontal region; scales in posterior loreal region about twice size of midorbital scales; eye large, its diameter contained in snout length about 1.8 times; eyelid with 2 rows of granules and one larger outer row of scales, last 8 to 12 are pointed; diameter of ear contained in diameter of eye about 2.8 times; ear opening small, not denticulate, scales on anterior and posterior margins rounded; rear of head granular; usually six supralabials and five infralabials to point below center of eye; mental bell-shaped, slightly longer than wide, its distal tip extends beyond posterior border of first pair of labials; postmentals much longer than wide, their median edges usually in narrow contact, nearly separated by posterior projection of mental; postmentals bordered across chin by very small granules.

Dorsum with irregular rows of small, oval tubercles that tend to be flat, posterior dorsal edge with faint keel; dorsal tubercles not regular enough to count with accuracy; postanal tubercles usually number four on each side; limbs with somewhat small, flattened scales; main portion of claw visible when viewed from below; terminal lamellae very small.

Color pattern in life: ground color yellowish tan; dorsum with profusion of dark brown, brown, light tan, and white granules and larger scales (tubercles) that tend to give entire dorsal color a sandy appearance; arms and legs similar to dorsum; dorsal surface of tail faintly banded with light gray bands on yellowish tan ground color; dorsal surface of head similar to dorsum; loreal region with larger diffuse spots of brown and tan granules; ventral surfaces brilliant white.

Variation. Snout-vent lengths of subadult and adult males vary from 33 to 56 mm (46.7), females from 32 to 58 mm (46.5), juveniles 23 to 31 mm (27.1), males plus females average 46.6 mm; tail length varies from 42 to 53 per cent of total length; postmentals number from two to four, two occurring in 90.6 per cent three in 8.0 per cent and four in 1.4 per cent of sample; postmentals contacting adjacent labials vary from none to two on each side, none in 4 per cent, one on one side and none on opposite side in 4 per cent, one on each side in 89.2 per cent one on one side and two on opposite side in 1.4 per cent and two on each side in 1.4 per cent of sample; number of scales across chin immediately following postmentals varies from 6 to 9 (7.4); scales across midorbital region range from 18 to 25 (20.8), across snout at level of third labial 18 to 26 (21.8); median and posterior scales bordering internasals vary from 7 to 12 (8.7), with median edges of internasals separated by granules in 99.2 per cent of sample; scales from nostril to eye range

from 10 to 15 (12.4); scales across venter vary from 21 to 38 (27.3), mainland populations from 26 to 38 (31.0), island populations 21 to 33 (25.8); scales from throat to vent range from 62 to 72 (66.3) in all populations; dorsal tubercular rows range from 10 to 14 (11.9) when arranged in somewhat regular rows, but majority of individuals have irregular rows; lamellae beneath fourth toe vary from 12 to 15 (13.3); terminal lamellae generally very small, but variable in size dependent upon soil type from which specimens are obtained; tail generally shorter than snout-vent length and always devoid of tubercular rows, ventral surface with all scales of equal size.

Dorsal color pattern variable, from light brown, brown, and white freckled appearance on yellowish tan ground color to dark brown to black reticulating lines on gray, tan or light brown ground color; broad, but indistinct brown bands are occasionally present in adults, more frequently in young and juveniles; a brownish line usually present from nostril to eye, occasionally extends to ear; ventral surfaces brilliant white.

Comments. There has been considerable confusion in the application of the name *microphyllus* to the original population Cope described in 1876. Cope described *microphyllus* and *inaequalis* in the same paper, but failed to make clear the type of digital expansion found in *inaequalis* that would separate it from *microphyllus*. Noble (1924) used the name *inaequalis* (= *microphyllus*) for populations inhabiting the sandy deserts of the coast, apparently being unable to distinguish between Cope's two species. Cope (1877) later described another species, *nigrofasciatus*, and in the same paper explained the differences in digital expansion between *microphyllus* and *inaequalis*, apparently overlooked by Noble and later workers.

Burt and Burt (1930), apparently confused by Noble's use of the name *inaequalis* for the sandy desert form, listed *microphyllus*, *inaequalis*, and *gerrhopygus* from Peru, but had misidentified a specimen of *gerrhopygus* as being *inaequalis*. They later (1931) perpetuated this mistake by listing *inaequalis* (= *gerrhopygus*) from Arequipa, Peru, and in part, confused specimens of *microphyllus* with *inaequalis* in northwestern Peru. This mistake was repeated by Donoso-Barros (1966).

Habitat and natural history. *Phyllodactylus microphyllus* is a widespread species, but generally restricted to the western sandy areas of the Sechura Desert, sandy and sand rubble beaches of the Peruvian coast and offshore islands. The absence of vegetation does not seem to restrict its distribution in the drier parts of Peru. We have found specimens in areas where vegetation was absent, but these individuals were found within one kilometer of the beach. The storm and intertidal zones of the beach are probably the principal sources of food. The absence of food elsewhere is a possible factor limiting the distribution of this species. In northwestern Peru where vegetation is more abundant this species has been taken 60 kilometers (airline) from the nearest beach.

During the day individuals have been found under rocks, cow chips,

boards, bones, paper, tin, and other objects strewn on sandy surfaces. In one instance individuals were found in open Indian graves where remnants of burial cloth were exposed. Some of these daytime retreats are often fully exposed to sunlight and the body temperatures of individuals found under these conditions are about 10°C higher than their nocturnal temperatures. In the vicinity of Culebras, this species was observed emerging just prior to complete darkness and actively foraging for about four hours. In the Cerro Illescas area of northwestern Peru this species was found foraging in leaf litter and on the branches and trunks of shrubs, mainly *Capparis avicennifolia*, during winter months. We observed this species foraging on guano mounds on Cerro Azul and it was reported from guano mounds on Isla Lobos de Afuera by Burt and Myers (1942).

The behavior of this species is similar to that of members of the genus *Coleonyx*. When disturbed, the tail is raised, back is arched, and it feigns an attack accompanied by noise and walks diagonally away with full side view of body exposed to a potential predator. The movements of this lizard are deliberate, somewhat slow, and when disturbed, it does not seem able to run rapidly. One individual was observed utilizing a small rock to scrape shedding skin from its body.

This species apparently lays a single egg per clutch. Preserved females contained a single egg in either the right or left oviduct.

One specimen was removed from the stomach of a snake, *Liophis* sp., but actual predation was not observed. Potential predators consist of ghost crabs, snakes, and foxes.

As in other species of *Phyllodactylus*, the nocturnal body temperatures of this species closely approximates that of the substratum.

Distribution. This species is known only from Peru. It ranges from the northwestern coastal village of Los Organos, southward to the coastal village of Cerro Azul, an airline distance of 1,150 km. The western part of the Sechura Desert of northwestern Peru is the only area where its range extends inland from the coast (fig. 2).

Specimens (277) have been examined from the following localities: *Ancash*: 2 km N Culebras LACM 48589-92, TCWC 28151-55. 12 km N, 1 km W Pativilca LACM 48570-72, TCWC 28148-50. 24.7 km N Pativilca MVZ 82145, 82231. *Lambayeque*: 11 km S Chiclayo MVZ 82181. Eten MCZ 18138, 17692-94, AMNH 28517-18. 10 km S Mocupe TCWC 28162. 3 km SE Morrope MVZ 82146. *Libertad*: Jequetepeque Valley ANSP 11364. 4 km N Pacanguilla LACM 48574, TCWC 28156-57. *Lima*: Ancon AMNH 36513-19. Cerro Azul LACM 48567-69, TCWC 28145-47. 7 km SSE Chilca MVZ 85430-34, 85436-38, 85440-41. Chorillos MJP 3 (no numbers). Cruz de Hueso USNM 75390. Isla San Lorenzo USNM 17541. Lima MJP 5 (no numbers), 3 km N San Antonio TCWC 28174. 5.5 km NE San Bartolo MVZ 85421-29. *Piura*: 1 km S Bayovar, Cerro Illescas MVZ 85353-61. 5 km SSE Bayovar MVZ 85342-52. 12 km S, 8 km E Bayovar MVZ 82157-61,

82270. 20 km SE Bayovar MVZ 85362-63. Isla Lobos de Afuera SDSNH 31123-53, USNM 38571-74. Isla Lobos de Tierra FMNH 34226(7), 34234 (5), 40113-14, AMNH 38753-55, UMMZ 83099 (2). 3.7 km ENE Los Organos LACM 48588, TCWC 28173. Negritos FMNH 5726-27, 8363, 8453-54. Paita AMNH 28461, HM 1499 (2). mouth of Parinas Valley FMNH 41543-45. 13 mi N Piura CAS 85163. 10 km E Piura MVZ 82162. Punta Aguja MVZ 82148-52, 82228, 82248. Reventazon MVZ 82153-56. 30 km SSE Sechura MVZ 82147. Talara FMNH 53891, 53894, 57457. 2 km E Talara LACM 48575-78, TCWC 28158-61. 2 km N Talara TCWC 28163. 3 km S Talara LACM 48579-86, TCWC 28164-71. 5 km S Talara LACM 48587, TCWC 28172. Tric Trac MVZ 82163-68, 85334-41.

***Phyllodactylus clinatus* sp. nov.**

Holotype. Adult female, MVZ 82227, collected by Raymond B. Huey, 19 July 1967. Type locality. Punta Aguja, 37 km SW Sechura, Department of Piura, Peru.

Definition: A small gecko with a known snout-vent length of 46 mm; dorsum with 10 to 12 rows of enlarged, trihedral tubercles; tubercles absent on tail, thigh, tibia, and forearm; granules absent between internasals; ear very large, 56.7 per cent of diameter of eye; ear strongly denticulated on anterior and posterior margins; terminal lamellae of digits large, truncate; all scales of median row beneath tail widened, rectangular (fig. 11b).

Diagnosis. This species may be distinguished from *P. heterurus*, *angustidigitus*, and *gerrhopygus* by the absence of an enlarged preanal plate; from *inaequalis* and *microphyllus* by much larger ear, dorsal rows of enlarged, trihedral tubercles arranged in regular series, and by a widened row of scales beneath tail; from *dixoni*, *pumilus*, *kofordi*, *sentosus*, *johnwrighti*, *reissi*, and *ventralis* by the absence of tubercles on tibia and much larger ear; from *lepidopygus* and *interandinus* by presence of a row of widened, rectangular scales beneath tail, larger ear, and small, flattened granular scales on tibia.

Description of holotype. Rostral twice as wide as high with short median groove about one-third depth of rostral; two internasals, somewhat rectangular, their median edges in broad contact, and bordered posteriorly by three granules and postnasal of each side; nostril surrounded by rostral, labial, internasal, and two postnasals; first labial in broad contact with ventral edge of nostril; deep depression between internasals, moderate depression in frontal region; scales in posterior loreal region about 2.5 times larger than midorbital scales; 22 scales across snout at level of third labial, 14 scales across anterior edge of orbits, 20 midorbital scales; eye large, its diameter contained in snout length 1.5 times; eyelid with two rows of granules and one larger outer row of scales, last 4 to 5 are pointed; ear diameter contained in eye diameter 1.8 times; ear opening large, denticulate; rear of head granular with larger intermixed tubercles; six supralabials and five infralabials to point below center of eye; mental bell-shaped, as wide as long; bordered posteriorly by two post-

mentals; postmental as wide as long, their median edges in broad contact, immediately followed by transverse row of 9 scales, followed by second row of 13 smaller scales; postmentals contact first labial only of each side.

Dorsum with 10 rows of enlarged, trihedral tubercles that are somewhat flattened; paravertebral row with 45 tubercles from head to base of tail, 24 between axilla and groin; paravertebral rows separated from each other by 4 to 6 rows of granules; 4 rows of dorsal tubercles reach to nape, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 3 granules; postanal tubercles number two on each side, indistinct; 26 scales across venter; 60 from throat to vent; dorsal surfaces of arm with granules and larger flattened scales; dorsal surface of thigh with granules and larger flattened scales, tibia with small flat granules; lamellae formula for hand 6-8-10-13-9, foot 7-9-11-14-10; claw hidden when viewed from below; terminal lamellae large, longer than wide, truncate; digits slender.

Measurements in mm: snout-vent length 46.0, axilla-groin length 19.0, length of leg 16.5, length of arm 14.4, length of tail 46.0, length of head 14.0, depth of head 4.9, width of head 8.7, length of snout 4.9, diameter of eye 2.3, diameter of ear 1.8, distance from eye to ear 3.6.

Color in life: ground color sand brown; dorsum with six narrow, chocolate brown bars interrupted along median line, ground color interspaces four to five times width of dark bars; sides of body with light tan spots between dark bars, tending to form ocellated pattern with network of fine brown lines intermixed; arms with chocolate brown reticulating lines, tending to form bands on upper arm; hind limb with five chocolate brown bands, one-third as wide as ground color interspaces; tail with 11 dark brown bands, ground color interspaces twice width of dark bands; head with dark brown parietal spot, rear of head with thin, dark brown reticulating lines: dashed and partly wavy line from rear of eye to hind limb, connecting with lower edge of dark body bars; supralabials with upper half heavily pigmented with dark brown, lower half and all of infralabials with suffusion of minute black dots; dark brown stripe from nostril to eye, tending to be black from eye to side of body; ventral surfaces with faint brownish dots scattered along sides, more dense on tail; general ventral color pale yellow.

Variation. Snout-vent length of juvenile male 28 mm, females vary from 34 to 46 mm (40.3); tail length about 45 to 50 per cent of total length; postmentals number 2 in all, contacting first labial only in all; number of scales across chin immediately following postmentals range from 6 to 9 (7.3); scales across snout at level of third labial range from 21 to 23 (21.8), midorbital scales from 19 to 22 (19.5); scales bordering posterior edge of internasals number 5 in all; scales from nostril to eye range from 13 to 15 (13.8); scales across venter vary from 26 to 32 (28.8), from throat to vent 60 to 64 (61.8); dorsal tubercular rows range from 10 to 12 (10.5); paravertebral tubercles from head to base of tail range from 42 to 46 (44.5), from axilla to groin 24 to 29 (27.5); lamellae beneath fourth toe range from 13 to 15 (14.0);

terminal lamellae of digits large and truncate in all; ratio of ear diameter to that of eye ranges from .500 to .653 (.567); ratio of ear diameter to distance between eye and ear ranges from .419 to .487 (.444).

Dorsal color pattern varies from distinct bands, broken along median line, to series of dorsolateral spots connected longitudinally by thin dark brown line; bands or spots (one side) vary from 6 to 8 (6.5); tail bands number 11 in only specimens with complete tail; limbs usually banded but bands may be obscured by dark ground color; ventral surfaces pale yellow in all specimens.

Habitat and natural history. Having taken only four individuals of this species, very little natural history information of the species could be obtained. All four specimens were taken from the vicinity of Cerro Illescas where *Capparis avicennifolia*, *C. scabrada* and mesquite are the dominant plants.

Three specimens were obtained in July and August of 1967. One was taken from a snap trap at the base of a small boulder near the edge of a cliff. The substratum was sandy, although it was only one-third meter from a fragmented shale area. One was captured on the trunk of a mesquite about one m above the ground. The third specimen was taken one afternoon under a small rock on sandy substratum, near rock outcrops and mesquite.

In spite of intensive collecting in this general area in 1968, only one additional specimen was obtained. It was found 2.5 m above the ground on a mesquite branch.

Distribution. This species is known only from the Cerro Illescas area of northwestern Peru (fig. 4).

Four specimens have been examined: *Piura*: 4 km SSE Bayovar MVZ 82271; 5 km SSE Bayovar TCWC 28332; 10 km SE Bayovar MVZ 82269; Punta Aguja MVZ 82227.

Phyllodactylus lepidopygus (Tschudi)

Diplodactylus lepidopygus Tschudi 1844-46, Untersuchungen uber die Fauna Peruana. Herp.: 38.

Discodactylus phacophorus Tschudi 1844-46, Untersuchungen uber die Fauna Peruana. Herp.: 38-39.

Phyllodactylus nigrofasciatus Cope 1877. Proc. Amer. Philos. Soc. Phila., 17:36.

Phyllodactylus variegatus Werner 1901. Abh. Mus. Dresden, 9(2): 2.

Holotype. NM 43, adult male, obtained by Tschudi prior to 1844. Type locality, Chorillos, Peru.

Definition. A moderate-sized gecko with known maximum snout-vent length of 55 mm; tibia and femur tubercles absent; ear denticulate on anterior margin; slightly enlarged tubercles among granules on rear of head; median row of scales on ventral surface of tail not enlarged; enlarged preanal scale absent; 10 to 16 (13.1) rows of enlarged trihedral tubercles on dorsum; tail length about 45 to 55 percent of total length, tail without enlarged tubercles;

terminal lamellae of digits moderately enlarged; body bands (may be broken on midline) 6 to 9 (7.2), tail bands 9 to 13 (11.0) (fig. 13a).

Diagnosis. This species is easily distinguished from *P. heterurus*, *angustidigitus*, and *gerrhopygus* by the absence of an enlarged preanal scale; from *kofordi*, *reissi*, *clinatus*, *dixoni*, *johnwrighti*, *pumilus*, *ventralis*, and *interandinus* by having all scales beneath the tail of equal size, rather than median row distinctly widened or enlarged; from *inaequalis* and *microphyllus* by having distinct dorsal rows of enlarged trihedral tubercles, rather than indistinct dorsal rows of small flattened tubercles or rows occasionally absent; from *sentosus* by the absence of tail, tibia, and thigh tubercles, rather than very large tubercles present.

Description. Rostral more than twice as wide as high; two internasals and two postnasals; nostril bordered by rostral, internasal, labial, and two postnasals; second supralabial separated from nostril by two granules and postnasal; postero-dorsal loreal scales about four times larger than interorbital scales; internasals slightly wider than long, bordered posteriorly by small scales; auricular opening very small, slightly denticulate, contained in snout length about eight times; eye large, contained in snout length about one and one-third times; rear of head granular with few larger, rounded tubercles; 7 to 9 supralabials and 5 to 6 infralabials to point below center of eye; mental slightly longer than wide, bordered posteriorly by two to three well defined postmentals; postmentals followed by irregular row of granular scales; eyelid with two rows of granules and larger palebral row of scales; last 2 to 5 scales in larger superciliary series bearing long spines; regular rows of longitudinal, enlarged keeled tubercles on dorsum, 8 rows reach to rear of head and 8 to base of tail; all rows equally spaced apart, no wide granular area separating paravertebral rows; four well defined postnasal tubercles on either side of anus in males; venter scales moderately differentiated from lateral body scales; no enlarged preanal shield; arm covered with flat imbricated scales, no enlarged tubercles intermixed with flattened scales; femur with flat, imbricated scales on dorsal and ventral surfaces, posterior-ventral surface with granular scales; lower leg similar to femur; terminal pads slightly longer than wide; claw short, hidden between terminal pads.

Variation. Specimens of this species with a minimum snout-vent length of 32 mm are considered young adults. In a sample of 36 specimens, 8 are less than 32 mm snout-vent length, 13 are males with snout-vent from 32 to 50 mm (40.8), 15 are females with snout-vent from 36 to 55 mm (46.8). The average snout-vent length for males and females is 44.0 mm.

The number of postmentals varies from two to four, two occurring 58.4 per cent of the time, three 38.9 per cent and four 2.7 per cent; number of scales bordering the postmentals range from 5 to 8 (6.9); number of scales across the midorbital region 15 to 21 (18.2); number of scales across the snout at the level of the third supralabial 17 to 22 (20.1); scales bordering the internasal shields posteriorly number 5 to 11 (6.7), with one or two small

azygous scales separating the internasals in 7 of 36 specimens; transverse venter scales number 26 to 34 (29.4), longitudinally 65 to 74 (69.6); scales from posterior edge of nostril to eye number 10 to 14 (11.4); fourth toe lamellae number 10 to 14 (11.5); dorsal tubercular rows number 10 to 16 (13.1); tubercles in paravertebral row from rear of head to base of tail number 42 to 53 (47.8), axilla to groin 24 to 34 (28.9); body bands or blotches number 6 to 9 (7.2), tail bands 9 to 13 (11.0).

The general ground color in life varies from a greenish brown to a deep blackish brown; dorsal body markings vary from black spots to brown cross-bands or light tan blotches; general appearance consists of light ground color with darker spots irregularly arranged; head with blackish line from nostril through eye to above arm, occasionally continuing along side of body to hind limb: top of head from prefrontal area to posterior tip of parietal region consistently darker than remainder of body in all specimens but one; one specimen has reversal pattern of dark ground color with light blotches; tail generally banded with alternating black or brown bands with light tan to whitish interspaces; interspaces usually about half the width of dark bands but occasionally as wide or wider than dark bands; regenerated tails usually reticulated with dark lines on tan ground color; juvenile pattern similar to that of adults; venter yellowish tan to yellowish brown with dark brown spotting along lateral edges or occasionally to center of venter; chin and throat creamy yellow in young and subadults, becoming progressively darker with suffusion of brownish dots in old adults; ventral surface of tail generally darker than venter.

Comments. We have examined the holotype of *P. lepidopygus*, three syntypes of *P. phacophorus*, holotype of *P. nigrofasciatus* and find that they are identical in general shape, size of head and body. Their scale characters are within the range of variation of a relatively large sample of *P. lepidopygus* from a single locality and we therefore consider *P. phacophorus* and *P. nigrofasciatus* as subjective synonyms of *P. lepidopygus*. The nine syntypes of *P. variegatus* were destroyed during the fire bombing of Dresden, Germany, during World War II and Werner's (1901) original description is the only evidence we have for a comparison of *P. lepidopygus* and *P. variegatus*. Werner's description agrees with the characters attributed to *P. lepidopygus*. His description agrees to some extent with the salient features of *P. reissi*, a species found further to the north. The major exception is the presence of tibia tubercles in *P. reissi*, absent in *variegatus*, and to a minor degree, the short outer row of dorsal tubercles in *P. reissi*, not so in *variegatus*. Werner gave the type locality as Lima (9 specimens) and Chanchamayo (1 specimen), both areas some 1,500 km south of the nearest locality where *P. reissi* has been taken. However, *P. lepidopygus* occurs in the vicinity of Lima and *P. variegatus* is considered a synonym of *P. lepidopygus*.

Habitat and natural history. This species has been found associated with the lomas vegetation of the Lima region, the drier *Tillandsia* association of the desert coast, and the coastal foothills to an elevation of 1,400 m. The

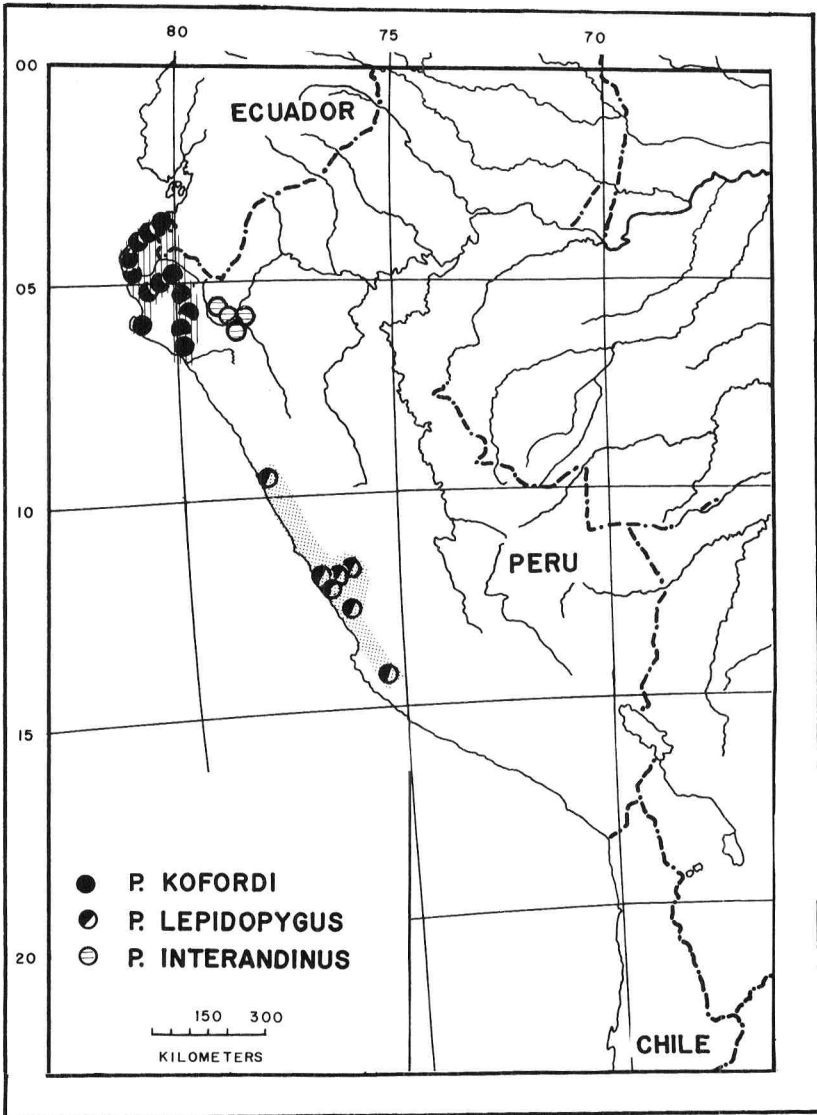


Figure 3. Distribution of *P. pumilus*, *P. kofordi*, *P. lepidopygus*, and *P. interandinus* in western South America.

microhabitat appears to be one of vertical surfaces of buildings, rock walls, large and small granite boulders, and crevices therein.

A series of 34 specimens taken by Huey, Dixon, and Wright from Lomas de Lachay were found exclusively on vertical surfaces of granite boulders, rock walls, or walls of buildings. No specimens were observed on rocks with abundant mossy growth, but lichen covered surfaces were utilized. Occasionally *P. lepidopygus* were seen in crevices or under smaller rocks resting on boulders during the day. This species became active as soon as it became dark, even on cold misty nights. The air temperature on 4 July 1967 was 13.2°C. approximately an hour and half after nightfall and seven geckos were taken subsequent to that time. Potential food items (e.g., *Porcellio*, spiders, moths) in the Lomas de Lachay region were plentiful on the rock surfaces at night. One specimen taken 24.7 km north of Pativilca was collected from a burro femur lying in a rolling sand hill region with few exposed surface rocks and *Tillandsia* as the only plant.

The only gecko observed in the Lomas de Lachay region was *P. lepidopygus*, but the rolling sand hill region 123 km north of Lima also contained *P. microphyllus*.

Of four specimens taken from the Asia area south of Lima, three were found actively foraging at night on a rock corral wall, and one was found on a small cerro on a rotting granite outcrop. All four were found on surfaces relatively free of heavy lichen growth.

Two individuals were found east of Chosica at an elevation of 1,700 m. Both specimens were taken from a wall of an abandoned adobe building that had been plastered. The coloration of both specimens was atypical, being almost translucent, without pattern, and inconspicuous against the light colored plaster. The two individuals had a more normal color pattern following a 24-hour period in a cloth sack.

An examination of the oviducts of preserved females reveals that this species lays a single egg per clutch. Natural nests were not observed but we suspect that eggs are deposited in cracks of large boulders in the Lomas de Lachay area. Several shells of *Phyllodactylus lepidopygus* eggs were found 40 km NNW Pativilca, 600 m, in dead cactus plants in a dry arroyo strewn with small boulders. No geckos were observed at this locality, but the location it within the known distribution of *lepidopygus*.

Distribution. The known range of this species is approximately 300 km north and 300 km south of Lima, and appears to be restricted to the rocky foothills from near sealevel to an elevation of 1,700 m (fig. 3).

Specimens (63) have been examined from the following localities: PERU. no specific locality BM 25440. *Ancash*: Chimbote Valley ANSP 11366. 24.7 km N Pativilca MVZ 82175. *Lima*: 2 km ESE Asia LACM 48473-74, TCWC 28142-43. 8 mi SE Chilca MVZ 85435. Chorillos NM 43. vicinity of Chorillos NM 41 (3). Chosica FMNH 34175. 26 km ENE Chosica LACM 48475, TCWC 28144. Lima MJP (3) unnumbered. Lomas de Lachay CAS

85143, LACM 48467-72, MVZ 82182-91, 82222-25, 82252-65, TCWC 28135-41. 20 km E Lurin MVZ 85411; Verrugas Canyon MCZ 26674. *Ica*: Ica FMNH 39367.

***Phyllodactylus interandinus* sp. nov.**

Phyllodactylus phacophorus, (part) Noble 1924, Occ. Paps. Bost. Soc. Nat. Hist., 5: 111.

Holotype. Adult female, TCWC 27914, collected by John W. Wright and James R. Dixon, 26 November 1968. Type locality, 4.8 km S (by road) Bellavista, 520 m, Department of Cajamarca, Peru.

Definition. A small gecko with a known snout-vent length of 47 mm; numerous rows of enlarged dorsal tubercles and tubercles in paravertebral row from head to tail and axilla to groin; terminal lamellae moderately large, digits short; distinctly banded, black, white, and yellowish green tail; tubercles absent on thigh, tibia, and forearm; distinct dorsal color pattern of three light and four dark longitudinal stripes (fig. 10a).

Diagnosis. This species is distinguished from *P. heterurus*, *angustidigitus* and *gerrhopygus* by the absence of an enlarged preanal shield; from *inaequalis* and *microphyllus* by having some scales beneath tail enlarged, and by numerous rows of enlarged trihedral tubercles on dorsum; from *clinatus*, *dixonii*, *ventralis*, *lepidopygus*, *kofordi*, *sentosus*, *johnwrighti*, *pumilus*, and *reissi* by presence of 65 or more tubercles in paravertebral row from head to base of tail, and distinct dorsal color pattern of light and dark stripes.

Description of holotype. Rostral twice as wide as high, its dorsal edge with vertical groove one-half depth of rostral; two internasals, somewhat rounded, their median edges in broad contact, bordered posteriorly by six granules and postnasal of each side; nostril surrounded by rostral, labial, internasal, and two postnasals; first supralabial in narrow contact with ventral edge of nostril; shallow depression between internasals and in frontal region; 12 scales on line between nostril and eye; scales of posterior loreal region about two times larger than midorbital scales; 22 scales across snout at level of third labial, 14 scales across anterior edge of orbits, 16 midorbital scales; eye large, its diameter contained in snout length 1.6 times; eyelid with two rows of granules and one larger outer row of scales, last three are pointed; ear contained in eye diameter 2.6 times; ear opening denticulate, but denticulate scales low and somewhat rounded; rear of head with subequal scales; five supralabials and four infralabials to point below center of eye; mental bell-shaped, slightly longer than wide, bordered posteriorly by three postmentals; postmentals rounded, their median edges in broad contact, immediately followed by transverse row of 8 scales, followed by second row of 12 smaller scales; postmentals contact first labial only on each side.

Dorsum with 20 longitudinal rows of enlarged trihedral tubercles, somewhat flattened, paravertebral row with 71 tubercles from head to base of tail, 44 between axilla and groin; paravertebral rows separated from each other by

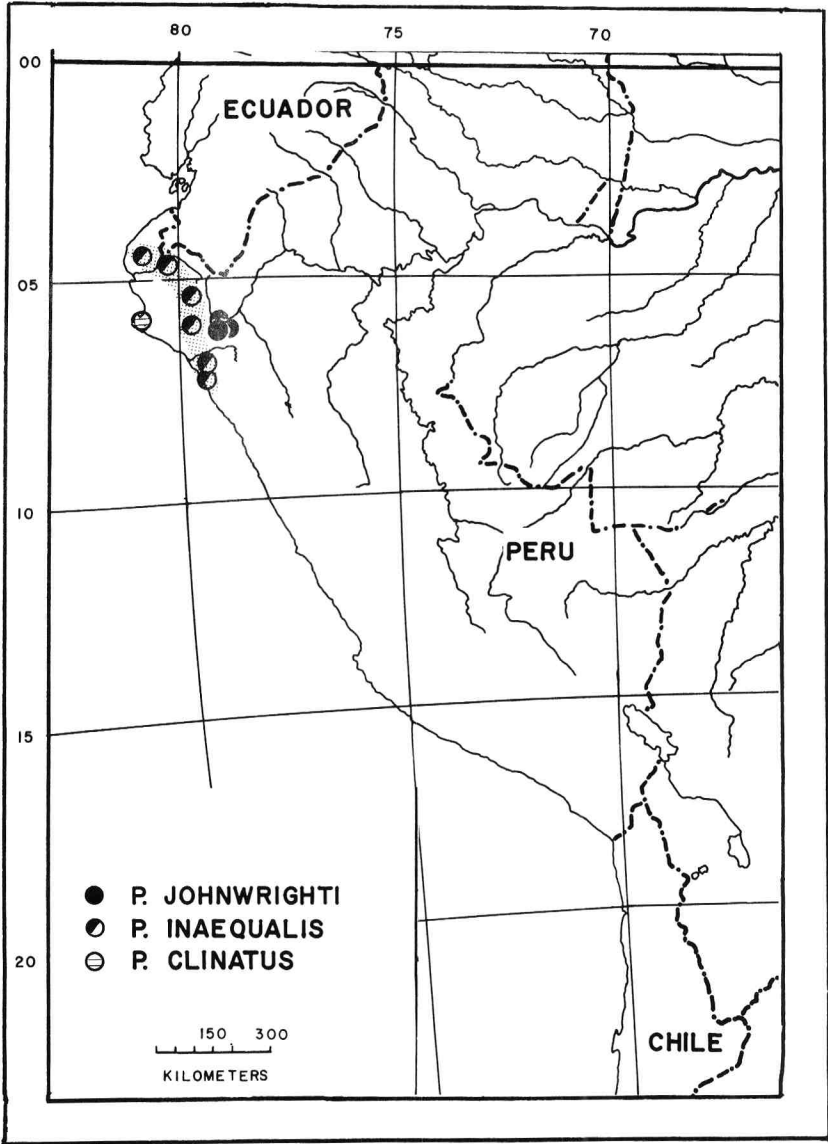


Figure 4. Distribution of *P. johnwrighti*, *P. inaequalis* and *P. clinatus* in western South America.

5 rows of granules, each tubercle of paravertebral row separated from preceding tubercle by 0 to 1 granule; 14 rows of tubercles extend across nape, 8 at base of tail; postanal tubercles number three on each side; 34 scales across venter, 58 from throat to vent; dorsal surface of arm with small flattened scales; dorsal surface of thigh without tubercles; tibia with subequal rounded, somewhat elevated scales; lamellae formula for hand 6-7-8-9-7, foot 6-9-10-11-10; claw barely visible when viewed from below; terminal lamellae moderately large, slightly longer than wide, rounded.

Measurements in mm: snout-vent length 41.0, axilla-groin length 18.6, length of leg 15.2, length of arm 12.1, length of tail 43.0, length of head 11.3, depth of head 5.2, width of head 8.1, length of snout 4.2, diameter of eye 2.6, diameter of ear 1.0, distance from eye to ear 3.3.

Color in life: ground color dark gray; dorsum with one median and two dorsolateral grayish white stripes, two dorsal and two lateral dark brown stripes; median light stripe from rear of head to base of tail, anterior part of median stripe bifurcates and extends anteriorly to above each eye; dorsal dark stripes tend to form series of loosely connected spots because of small clusters of grayish white spots scattered in dark fields; lateral dark stripe extends from snout to groin; limbs heavily mottled with grayish white and grayish black spots; tail with 11 black bands, posterior edge of each black band with white tipped scales; interspaces three times width of black bands, greenish yellow; dorsal surface of head with diffuse dark brown lines; ventral surfaces dusky, chin generally whitish, each scale with black dots.

Variation. Snout-vent lengths of subadult and adult males range from 32 to 45 mm (39.2), females 33 to 47 mm (41.1), young and juveniles 22 to 30 mm (29.0), males plus females average 40.1 mm; tail lengths vary from 48 to 55 per cent of total length; postmentals range from two to four, two occurring in 58.4 per cent, three in 38.9 per cent, and four in 2.7 per cent of sample; chin scales bordering postmentals range from 5 to 8 (6.9); postmentals contact first labial only of each side in 99.6 per cent, first labial on one side, none on opposite side in 0.4 per cent of sample; scales bordering internasals number 5 to 7 (6.2); scales from nostril to eye vary from 9 to 12 (10.8); scales across snout at level of third labial range from 22 to 27 (24.3), mid-orbital scales 18 to 22 (20.3); scales across venter vary from 26 to 33 (29.6), from throat to vent 56 to 65 (60.8); fourth toe lamellae range from 10 to 12 (11.6); longitudinal rows of dorsal tubercles vary from 14 to 22 (17.4); tubercles in paravertebral row from head to base of tail range from 65 to 85 (70.1), between axilla and groin 35 to 60 (40.7).

Color pattern consists of one median and two dorsolateral grayish white to yellowish tan stripes, separated by two dorsal and two lateral grayish brown to grayish black stripes; dark stripes usually bifurcates on nape, each arm extending anteriorly to posterior edge of eye or to tip of snout; broad, dark brown stripe usually present from snout to rear of head, lying between dorsolateral light stripes; ventral surfaces usually dusky with black dots on each

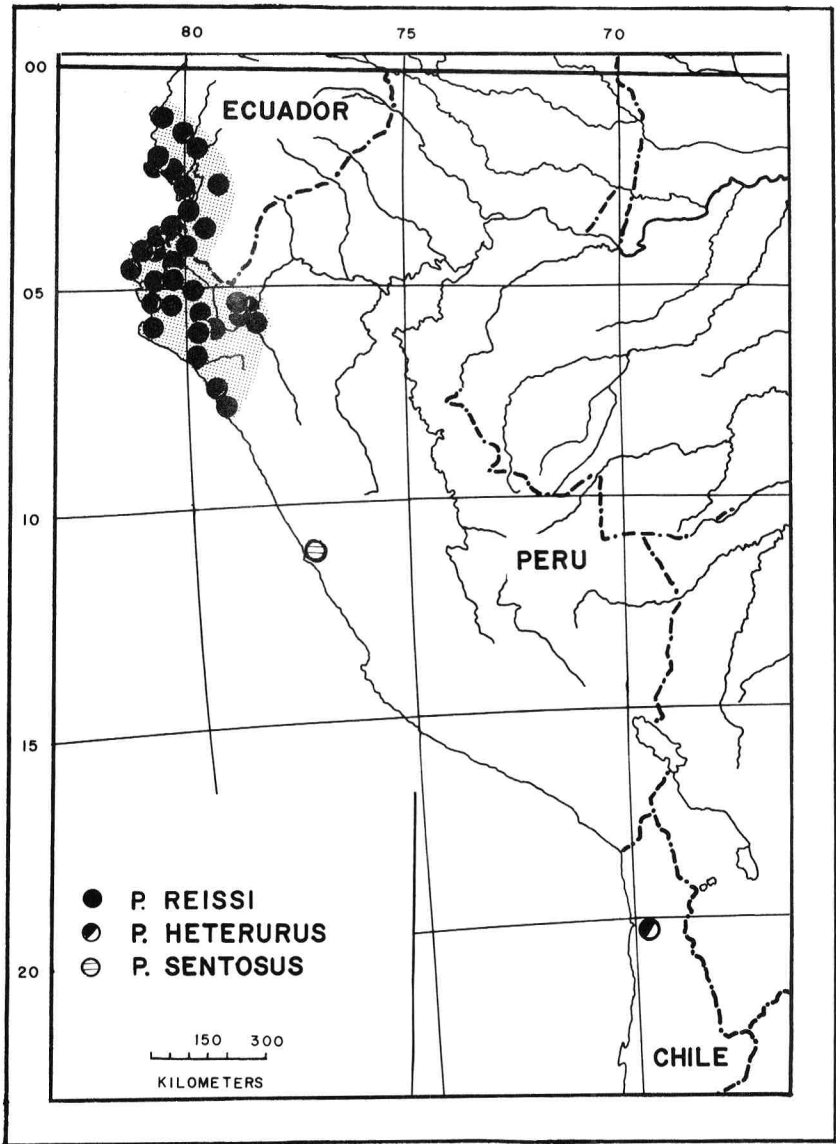


Figure 5. Distribution of *P. reissi*, *P. heterurus* and *P. sentosus* in western South America.

scale, chin and throat generally lighter in color than remainder of body; dorsal surface of tail with 11 to 16 narrow black bands edged with white posteriorly; broad interspaces bright reddish orange in juveniles, yellowish orange in subadults, yellowish green in adults.

Comments. Noble (1924) labeled a relatively large series of specimens from northwestern Peru as *P. phacophorus*, but the majority of the specimens are referable to *P. interandinus*. A critical examination of the entire series reveals four species were present in the collection, *interandinus*, *johnwrighti*, *kofordi*, and *reissi*.

Habitat and natural history. Noble (1924) recorded taking *phacophorus* (= *interandinus*) and *magister* (= *reissi*) from houses and deserted huts in Bellavista. We were unable to obtain *interandinus* in Bellavista but found *reissi* on the walls of houses. *Phyllodactylus interandinus* was abundant on a thorn scrub hillside a few kilometers south of Bellavista. Standing, dead *Cereus* sp. are the principal daytime retreats of this species with as many as seven individuals occupying one plant. Some individuals were taken as high as two meters above the ground, but the majority of specimens were found within one meter of the ground, usually beneath the bark, in the hollow trunks or branches. *Phyllodactylus reissi* and *interandinus* were taken from the same cactus plant, but the former species was not abundant. The distribution of *interandinus* is spotty, for similar areas of vegetation on other hillsides yielded only *reissi*. Hillsides and valleys were examined in the Department of Amazonas, east of the Rio Marañon, but only *reissi* were found in abundance. Only six individuals of *interandinus* were found east of the river, taken beneath rotting agave stumps and dead cactus litter. A total of 79 *reissi* were taken east of the river in a wide variety of habitats, including agave.

There seems to be potential competition between these two species for space but not for food. *Phyllodactylus reissi* is primarily scansorial while *interandinus* forages on the ground. Eggs of both species were found in a variety of rotting debris, but *reissi* eggs were far more numerous than those of *interandinus*.

An examination of preserved females of both species indicates that *P. interandinus* lays one egg per clutch and *reissi* two eggs per clutch.

There are distinct behavioral differences between *P. interandinus* and *reissi* when suddenly exposed to sunlight while in their daytime retreats. *Phyllodactylus interandinus* remains motionless for a few seconds, then seeks cover under debris within a few centimeters of where it was uncovered. *Phyllodactylus reissi* immediately runs up or down the plant upon which it was exposed, or jumps to the ground and runs to the nearest cover to hide.

The uneven distribution of *P. interandinus* in the Marañon Valley suggests that its niche requisites are more restricted than those of *reissi*.

Distribution. This species is an inhabitant of the Chinchipe, Marañon, and Utcubamba river valleys of the departments of Amazonas and Cajamarca, Peru. The locality of a series of specimens in the Museum of Zoology, Uni-

versity of Michigan, is given as Sullana, Peru. This locality is approximately 70 km west of the Andes, and lies at the north end of the Sechura Desert. The specimens are in a similar state of color and preservation as those collected by Noble in 1916. We believe this locality to be in error, and represent some of the specimens taken by Noble from the Chinchipe or Marañon river valley (fig. 3).

Specimens (149) have been examined from the following localities: PERU: *Amazonas*: 17 km S Bagua Chica LACM 48538, TCWC 28087. 10 km WSW Bagua Grande MVZ 82178-80, 82251. *Cajamarca*: Bellavista AMNH 39338, 39341-42, MCZ 18139, 18140(80), SMFM 8295, TCWC 24924-27. 4.8 km S Bellavista LACM 48519-37, 48539, TCWC 27914, 28066-68, 28070-86. Perico AMNH 28428-36. *Piura*: Sullana UMMZ 59034(4) (in error).

***Phyllodactylus kofordi* sp. nov.**

Holotype. Adult male, TCWC 27912, collected by James R. Dixon and John W. Wright, 19-20 Nov. 1968. Type locality. 7 km S Motupe, Cerro de la Vieja, Department of Lambayeque, Peru, 150 m elev.

Definition. A small gecko with a maximum known snout-vent length of 46 mm; tibia and femur tubercles present; ear denticulate on anterior and posterior margins; moderately enlarged tubercles on rear of head intermixed among granules; median row of scales below tail distinctly widened; enlarged preanal scale absent; 12 to 14 (12.1) rows of enlarged trihedral tubercles on dorsum; tail 50 to 55 per cent of total length; tail with an 8-6-4-2 or 6-6-4-2 reduction of enlarged tubercles per whorl from base to distal half of tail; terminal lamellae of digits moderately enlarged, truncate; body markings of three types, with spots, dots, or uniform coloration; tail markings of two types, uniform or banded; trihedral tubercles of tibia greatly enlarged (fig. 11a).

Diagnosis. This species may be distinguished from *P. heterurus*, *angustidigitus* and *gerrhopygus* by the absence of an enlarged preanal plate; from *johnwrighti*, *pumilus*, *interandinus*, *clinatus*, *inaequalis*, *lepidopygus*, and *microphyllus* by the presence of greatly enlarged trihedral tubercles on the dorsum, thigh, tibia, and forearm and by whorls of tubercles on the entire length of dorsal surface of the tail; from *sentosus* by having much larger terminal lamellae, smaller dorsal tubercles, and smaller snout-vent length; from *reissi* by the presence of tail tubercles, tubercles on the thigh, smaller body size (maximum 46 mm rather than 75 mm), fewer paravertebral tubercles from rear of head to base of tail (31 to 36 rather than 46 to 60), and fewer paravertebral tubercles between axilla and groin (16 to 21 rather than 28 to 38); from *dixonii* and *ventralis* by the latter two characters and smaller maximum snout-vent length.

Description of holotype. Rostral twice as wide as high; depression between internasals continues posteriorly through frontal and interorbital regions; internasals bordered posteriorly by 5 granular scales; 18 scales across

snout between third labials, 13 across snout between second labials; 14 between middle of orbits; 11 scales between eye and nostril; posterodorsal loreals slightly more than three times larger than interorbital scales; two postnasals; auricular opening strongly denticulate, two or three auricular scales bearing long spines, projecting posteriorly from anterior margin; eye diameter slightly less than two times the snout length; ear diameter contained in eye diameter three times, in snout length 5 times; second supralabial separated from nostril by two loreal scales and postnasal; antero-dorsal border of first supralabial forms projecting edge bordering nostril below; 6 supralabial and 5 infralabial scales to center of eye; mental slightly longer than wide, bordered posteriorly by two postmentals which contact only the first labial on one side and none on the opposite side; postmentals followed by irregular transverse row of 6 scales, followed by second row of 10 smaller scales;

Dorsum with 12 longitudinal rows of enlarged, keeled tubercles, 8 reach to rear of head, 6 reach base of tail; 28 scales across venter; 56 from gular region to vent; venter scales abruptly differentiated from lateral and dorsal scales, about 5 to 6 times larger; 6 rows of enlarged tubercles on anterior six whorls of tail, separated longitudinally by two annular rows of flat scales; distal half of tail with rapid reduction of tubercular rows, 6-4-2-0; ventral surface of tail with longitudinal row of 43 widened scales, about twice to three times larger than adjoining scales; three postanal tubercles on either side of vent; dorsal surface of femur and tibia with large trihedral tubercles intermixed with granular scales; postero-ventral surface of femur granular; upper arm with large, flat scales; forearm with enlarged tubercles intermixed with smaller flattened scales; terminal pads slightly longer than wide; claw not extending beyond pad tips nor visible from below; lamellae formula for hand 7-8-9-11-8, foot 7-9-10-12-11.

Measurements in mm: Snout-vent length 44.0; head width 9.0; head length 13.1; head depth 6.4; axilla-groin length 21.2; tail length 47.0; leg 18.6; arm 12.5; snout length 5.0; eye diameter 2.7; ear diameter 1.2; distance from eye to ear 4.1.

Color in alcohol: Narrow broken, diagonal and transverse black lines across dorsum, 13 complete bands on tail; dark brownish stripe from nostril through eye to arm insertion; each enlarged dorsal tubercle flecked with black; venter immaculate, pale white; labials stippled with brown; limbs faintly spotted with brown.

Variation. Snout-vent length of subadult and adult males ranges from 30 to 45 mm (38.0), females from 30 to 46 mm (38.6), juveniles from 18 to 29 mm (25.4), males and females together average 38.3 mm; postmentals vary from two to four, two occurring 104 times, three 5 times, and 4 one time; postmentals contact the first labial only in 89.8 per cent of the sample, first and second labial in 11.2 per cent; number of scales immediately following postmentals across the chin vary from 5 to 8 (6.7); scales across the midorbital region range from 13 to 19 (15.8), across the snout at the level

of the third labial 16 to 20 (17.3); number of scales bordering the internasals vary from 4 to 8 (5.8) with an azygous scale separating the internasals in 14 of 110 specimens; transverse rows of scales across the venter number 22 to 30 (25.0), longitudinally 47 to 56 (50.6); dorsal tubercular rows number 12 to 14 (12.1); paravertebral tubercles from head to tail number 31 to 36 (34.0), from axilla to groin 16 to 21 (18.0); scales on a line between nostril and eye number 10 to 13 (11.5); lamellae beneath fourth toe number 11 to 13 (11.5); body markings (if present) number 5 to 8 (7.1); tail bands (if present) 8 to 11 (9.9).

Tubercles on the dorsum, tibia, and thigh usually much enlarged, strongly keeled and trihedral; tail tubercles large, somewhat flattened, keeled and elevated posteriorly.

Color pattern consists of three distinct types; (1) presence of distinct black spots, lines or blotches, (2) distinct but very small black dots, (3) uniform coloration; ground color generally pale brown in all specimens; in those with dorsal markings, the head is usually spotted with profusion of dark brown on ground color; dark brown to black stripe present from nostril through eye to above arm or slightly beyond; tail generally banded with dark brown to black on proximal three-fourths of tail, black and white on distal one-fourth; those with uniform pale brown dorsal color occasionally have dark lateral head stripe and faint tail bands; venter of all specimens pale white to white; chin, throat, and chest with suffusion of light brown flecks on each scale; ventral surface of tail usually heavily suffused with dark brown to black flecks, much darker than venter color.

Comment. This species is named in honor of Carl Koford, who has added much to our knowledge of the mammalian and reptilian fauna of Peru in the past twenty years.

Habitat and natural history. This small gecko is widespread and abundant in northwestern Peru. It has been found in every type of plant community from sea level to 650 m, except for the main dune areas of the Sechura Desert. This species is primarily a ground forager although it has been taken occasionally on boulders and plants. The daytime retreats of this lizard are usually holes beneath rocks, cracks in the ground, holes in sand banks, leaf litter at the base of plants, under or in hollow limbs of cacti, under bark of shrubs or stumps of rotting trees, in beach debris or trash dumped along the roadside. Occasionally a few individuals were found beneath exfoliating flakes of granite.

Eggs of this species were found under rotting cacti (mainly *Cereus*) in the Piura and Tumbes areas. One dead *Cereus* sp. plant contained 15 eggs of *P. kofordi* and 4 eggs of *reissi*. Eggs were not found in other types of cactus litter, nor in debris of acacia and mesquite. It appears that dead *Cereus* sp. affords the necessary protection for the survival of the eggs and this plant is sought out by females for egg deposition. This species lays one egg per clutch. Captive females laid a single egg and preserved females contained only one egg.

Gravid females and small juveniles were found in July, August, Novem-

ber, and December, indicating at least summer and winter breeding periods. Diurnal body temperatures were 8°C above the lizard's nocturnal temperatures during foraging periods.

This species is sympatric with *P. reissi* throughout most of its range, with *reissi* and *inaequalis* along the desert foothills, and with *reissi*, *clinatus*, and *microphyllus* in the Cerro Illescas area near the coast. Somewhere between Los Organos and Cancas (on the northwest coastline) the northern distribution of *microphyllus* terminates, and the habitat (beach dunes community) left vacant is effectively taken over by *kofordi* from Cancas to the Ecuadorian border. Both were found in the same general microhabitat near Talara (beach dunes) but *microphyllus* was much more abundant than *kofordi*.

Distribution. *Phyllodactylus kofordi* is a Peruvian species, found on the periphery of the Sechura Desert, western foothills of the Andes, and along the coast from Eten north to the Ecuadorian border. It probably occurs in the southwestern part of Lojas and the southern part of El Oro Departments, Ecuador (fig. 3).

Specimens (167) have been examined from the following localities: *Lambayeque*: Chiclayo MVZ 82221. Eten BMNH 1900.2.26.1. 5 km SSW Motupe MVZ 82209. 7 km S Motupe MVZ 82249-50, LACM 48540, 48559-66, TCWC 27912, 28107-14. 7.2 km W Naupe LACM 48543-46, TCWC 28117-20. 22 km E Olmos LACM 48541-42, TCWC 28115-16. *Piura*: Bayovar FMNH 9803. 1 km S Bayovar, Cerro Illescas MVZ 85268, 85290-91, 85293-304. 4 km SSE Bayovar MVZ 82203-05, 82230. 5 km SSE Bayovar MVZ 85287-89. 12 km S, 8 km E Bayovar MVZ 82176. Cerro Amotape MVZ 82193-94, 82210-16, 82233-37, 82239-40, 82242, 82281, 82284. Chongollapi AMNH 28465. 8 km S, 8.4 km SSE Chulucanas LACM 48547, TCWC 28121. Fondo MVZ 82274. 2 km NE Las Lomas MVZ 85259, 85278-84. 3 km ENE Las Lomas LACM 48556-58, TCWC 28131-34. 5 km E Las Lomas MVZ 82243-47, 82296. 30 mi S Lobitos BMNH 1932.9.5.1-2. 2 mi S Lobitos BMNH 1926.3.24.5. Negritos FMNH 8362. Paita AMNH 28460, 28462-64. Punta Aguja MVZ 82192, 82226, 82266-69. Reventazon MVZ 82229. 40 km WNW Sullana LACM 48548, TCWC 28122. Talara FMNH 57455. 2 km N Talara TCWC 28123. Tric Trac MVZ 82206, 85252-58, 85260-67, 85269-77, 85285, 85292, 85305-06. *Tumbes*: 1.2 km S Cancas LACM 48549-50, TCWC 28125-27. 1.2 km S, 1 km E Puerto Pizarro LACM 48551-55, TCWC 28128-30. Quebrada Seca FMNH 9810, TCWC 28124.

***Phyllodactylus ventralis* O'Shaughnessy**

Phyllodactylus ventralis O'Shaughnessy 1875. Ann. & Mag. Nat. Hist., (4)16:263.

Phyllodactylus mulleri Parker 1935. Ann. & Mag. Nat. Hist., (10)15:483.

Phyllodactylus underwoodi Dixon 1962. Southwest. Nat., 7:218.

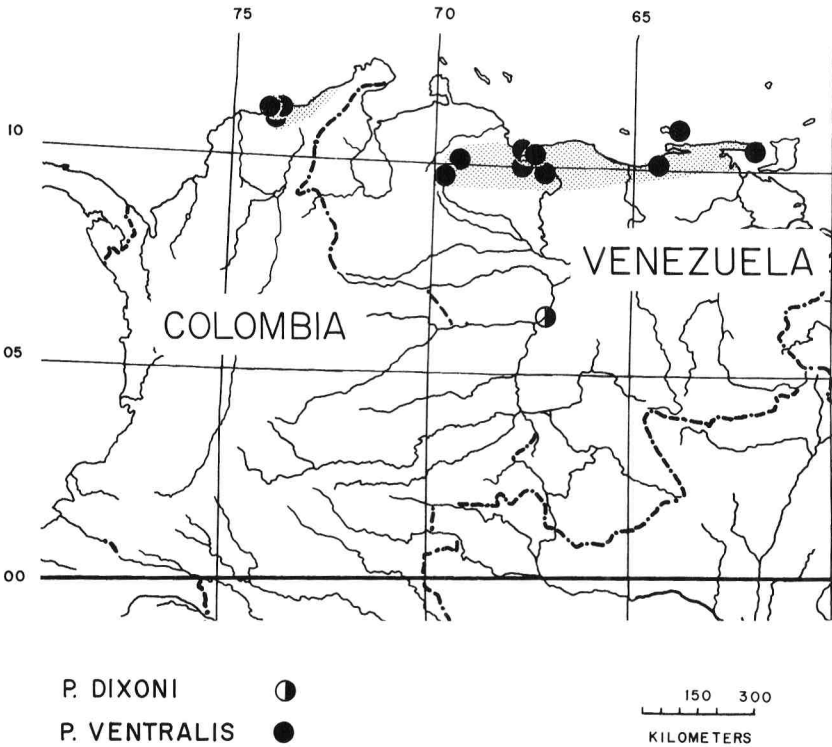


Figure 6. Distribution of *P. dixonii* and *P. ventralis* in northeastern South America.

Holotype. Adult male, BMNH 53.6.1.33, collector unknown, date of collection unknown. Type locality, Island of Jamaica (in error).

Definition. A large gecko with a maximum known snout-vent length of 75 mm; tibia and thigh tubercles present; ear denticulation usually present; enlarged preanal scale absent; terminal lamellae of digits distinctly widened and usually truncate at tips; median row of scales beneath tail distinctly widened; dorsal rows of enlarged tubercles close together, trihedral, and strongly carinate; six to eight rows of tubercles across base of tail; rear of head with rounded tubercles dispersed among granular scales (fig. 14a).

Diagnosis. *Phyllodactylus ventralis* is distinguished from *heterurus*, *gerhopygus*, and *angustidigitus* by the absence of an enlarged preanal scale; from *inaequalis* and *microphyllus* by the presence of regular rows of large trihedral, strongly keeled dorsal tubercles; from *clinatus*, *lepidopygus*, and *interandinus* by the presence of large tibia tubercles; from *johnwrighti*, *pumilus* and *reissi* by the presence of large tubercles on forearm; from *sentosus* by having terminal digital lamellae distinctly widened and enlarged; from

kofordi by greater maximum snout-vent length of 75 mm, rather than 46 mm; and 19 or more paravertebral tubercles between axilla and groin; from *dixoni* by having 24 or less scales across venter, rather than 26 or more, and dorsal tubercles four or more times the size of those in *dixoni*.

Description. Rostral about one and one half times higher than wide; two internasals, bordered posteriorly by small granular scales and postnasal of each side; nostril surrounded by rostral, labial, two postnasals and internasal; ventral edge of nostril scale in broad contact with first labial; deep depression between internasals and in frontal region; scales of posterior loreal region six to seven times larger than midorbital scales; eye large, contained in snout length about two times; eye brille with one to two rows of granules and one larger outer row of scales, posterior half are pointed; ear diameter contained in eye diameter about three times; ear opening slightly denticulate anteriorly, none posteriorly; rear of head with very large tubercles dispersed among granular scales; supralabials usually six to seven and infralabials five to six to a point below center of eye; mental slightly longer than wide, somewhat triangular in shape.

Dorsum with regular longitudinal rows of very large, trihedral tubercles, 10 to 14 rows reach nape, 6 to 8 rows reach base of tail; paravertebral rows of tubercles separated along median line by four to five rows of granules; postanal tubercles usually number three to four and very distinct in adult males.

Forearm with large trihedral tubercles dispersed among granular scales; upper arm with large flat scales; dorsal surface of thigh and tibia with 10 to 20 very large tubercles dispersed among granular scales; terminal digital lamellae large, either rounded or truncate; claw short, hidden when viewed from below.

Variation. Snout-vent lengths of adult males from 50 to 74 mm (62.4), adult females from 52 to 75 mm (62.3), subadults 40 to 45 (42.2), juveniles 24 and 29 mm; postmentals normally two, three occurring once in 22 specimens; postmentals contact first labial only in 25 per cent; first and second labials in 75 per cent of sample; scales bordering internasals vary from 4 to 6 (5.1); scales from nostril to eye vary from 9 to 12 (10.3); scales across snout at level of third labials vary from 17 to 23 (19.4); midorbital scales 12 to 17 (14.4); dorsum with 14 to 19 (16.4) longitudinal rows of enlarged trihedral tubercles; paravertebral tubercles from head to base of tail vary from 34 to 49 (41.2), axilla to groin 19 to 25 (22.1); venter scales from gular region to vent vary from 46 to 54 (52.0), across venter from 18 to 24 (20.6); fourth toe lamellae vary from 12 to 14 (13.6).

Color pattern varies from seven to 10 narrow, undulating, dark brown cross bands on a light brown to tan ground color, to a linear series of 10 to 20 dark brown spots on a yellowish brown ground color; dorsal surface of head generally brown with or without dark brown spots or reticulating lines;

side of head usually with a dark brown line from nostril through eye to arm insertion, bordered above and below by whitish lines or ground color; labials usually spotted or mottled with brown and dirty white; venter dirty white to yellowish brown.

Comments. In 1962 one of us (Dixon) described a new species, *Phyllodactylus underwoodi*, from the island of Grenada, Windward Islands. The holotype is the only available specimen and is unique in several features of scalation. Miss Alice G. C. Grandison (*personal communication*) informed us that there was an error in the labeling of this specimen, and it should have been labeled as Colombia. This specimen was a part of a relatively small collection made by F. A. Simons, purchased from a Mr. Janson by the British Museum of Natural History, and bore the locality New Grenada.

Dixon (1962) noted the similarity of *P. underwoodi* to *ventralis*, but it differed in three major scale characters. It is now apparent that *P. underwoodi* is likely an aberrant *ventralis*, having three postmentals, 14 rows of enlarged dorsal tubercles, and six rows of tubercles across the base of the tail. No specimens of *ventralis* from Colombia or Venezuela have this combination of scale counts. However, only 22 specimens of *P. ventralis* have been examined, and additional material may reveal a wider range of variation.

Habitat and natural history. This species has not been collected by either of us, therefore we rely upon information from the literature and from personal observations of others. Ruthven (1922) records *P. ventralis* from houses, buildings, under stones and bark of trees. Two specimens were found in a dry thorn forest and one in a thorny scrub and cacti association under a stone. Mechler (1968) found three specimens in debris of an abandoned house in Bonda, Colombia. Janis A. Roze (*personal communication*) states that *P. ventralis* occurs in dry, semixerophytic areas, but occasionally penetrates more moist habitats where cactus and thorny vegetation is replaced by a rich variety of shrubs and trees. Roze (1964) states that *P. ventralis* is often found in occupied houses, in abandoned buildings, and trees near buildings. Roze indicated that competition between *Thecadactylus rapicauda* and *P. ventralis* for human dwellings is being won by *T. rapicauda*.

Distribution. This species is found in the dry thorn forests and savannahs of northern Venezuela and Colombia (fig. 6).

Specimens (22) have been examined from the following localities: COLOMBIA. *Magdalena*: Bolivar UMMZ 54737. "Grenada" BMNH 1880.2.26.6. Santa Marta UMMZ 48177. Santa Marta Mountains MCZ 24881, UMMZ 45462-63. VENEZUELA. *Anzoátegui*: Barcelona MBUCV 3144. *Aragua*: Maracay MCZ 39980. *Carabobo*: Caizuire MBUCV 3151. Isla de Burro MBUCV 3143. *Falcón*: Coro MBUCV 3148. *Guárico*: San Juan de los Morros MBUCV 3149. Sosa MBUCV 3145. *Portuguesa*: Acarigua MCZ (unnumbered). Aparicion MBUCV 3146. *Sucre*: Isla Patos BMNH 1935.10.1. 10-11, 1940.2.15.1, 1945.11.1.41-42. Puerto de Hierro MCZ 50744-45.

Phyllodactylus dixoni Rivero-Blanco and Lancini

Phyllodactylus dixoni Rivero-Blanco and Lancini 1968. Mem. Soc. Cienc. Nat. La Salle, 27:168.

Holotype. Adult female, MBUCV III-8.450, collected by Juhani Ojasti in a cave on 5 October 1964. Type locality, Desembocadura del Rio Parguaza, afluyente del Orinoco Medio en el Estado Bolivar, Venezuela.

Definition. A large gecko with a maximum known snout-vent length of 76 mm; tibia, thigh, and forearm tubercles present; ear with little or no denticulation; enlarged preanal scale absent; terminal lamellae of digits distinctly widened and truncate; median row of scales beneath tail distinctly widened; dorsal rows of enlarged tubercles somewhat small, low and slightly trihedral; each dorsal row of tubercles separated from the other by three to five rows of granules; six to eight rows of dorsal tubercles across base of tail; rear of head with rounded tubercles dispersed among granular scales, almost subequal in size (fig. 14b).

Diagnosis. *Phyllodactylus dixoni* may be distinguished from all other mainland species except *ventralis*, by having no enlarged preanal scale; regular dorsal rows of keeled tubercles; presence of tubercles on forearm, thigh and tibia; distinctly enlarged and widened terminal digital lamellae; large maximum snout-vent length of 76 mm; 23 or more paravertebral tubercles between axilla and groin; from *ventralis* by having dorsal tubercles about one fourth the size of those of *ventralis*; 26 or more scales across the venter rather than 24 or less.

Description. Rostral twice as wide as high, its dorsal edge with median vertical groove about one half depth of rostral; two internasals, bordered posteriorly by small granules and postnasal of each side; nostril surrounded by rostral, labial, internasal and two postnasals; first labial in broad contact with ventral edge of nostril scale; shallow depression between internasals, moderate depression in frontal region; scales in posterior area of loreal region about three to four times larger than scales in midorbital region; eye large, its diameter contained in snout length about 1.5 times; eye brille with two rows of granules and one larger outer row of scales, last five to eight pointed; ear diameter contained in eye diameter about two times; ear opening without denticulation, scales on posterior and anterior borders rounded; rear of head with granular scales with slightly larger rounded and elevated scales intermixed; supralabials six to seven and infralabials five to six to a point below center of eye; mental bell shaped, about as wide as long; two postmentals, slightly longer than wide and in contact on median line; postmentals contact only first labial.

Dorsum with regular rows of enlarged, keeled tubercles that are somewhat oval in outline; paravertebral rows separated from each other by four to five rows of granules; 10 rows of dorsal tubercles reach nape, 6 to 8 reach

base of tail; postanal tubercles number three to four on each side in males; venter scales abruptly differentiated from lateral body granules.

Dorsal surface of upper arm with flattened scales; posterodorsal surface of forearm with tubercles interspersed among small scales; dorsal surface of thigh with 15 to 25 tubercles dispersed among smaller flattened scales; tibia with large tubercles dispersed among granular scales; terminal lamellae large, somewhat truncate, about twice as long as wide; claw long, visible when viewed from below.

Variation. The known snout-vent lengths of adults range from 56 to 76 mm (67.8), subadults 39 and 46 mm, juvenile lengths unknown; scales bordering postmentals vary from 5 to 8 (6.1); scales from nostril to eye vary from 11 to 12 (11.3); scales across snout at level of third labials vary from 17 to 20 (18.6), midorbital scales 15 to 19 (17.5); scales bordering internasals vary from 5 to 6 (5.1); longitudinal rows of enlarged dorsal tubercles vary from 13 to 16 (14.9); number of paravertebral tubercles from head to base of tail vary from 41 to 50 (46.7), axilla to groin 23 to 26 (24.7); venter scales from gular region to vent vary from 59 to 66 (61.7), across venter 26 to 28 (27.1); fourth toe lamellae vary from 11 to 13 (11.3).

Dorsal color pattern usually consists of five to eight undulating, dark brown cross bands on a brownish gray ground color from occiput to base of tail; tail banded with dark brown and light gray in juveniles, sometimes irregular bands or spots in adults; head usually brownish gray with a suffusion of dark brown spots; labials spotted with dark brown; venter usually brownish cream; lower sides of body brownish yellow; ventral surfaces of toes dark brown.

Habitat and natural history. Dr. Janis Roze (*personal communication*) states that the type series of *P. dixonii* was taken from beneath flakes of black basaltic rocks. The flakes were associated with immense, grayish black rock bluffs some 500 meters from the mouth of the Rio Parguaza. The immediate vicinity was essentially void of vegetation except for a few scattered shrubs and bromeliads. During the day, the temperature of the rocks reached 60°+C and the lizards took refuge beneath flakes or within cracks of boulders.

The majority of lizards were taken by breaking off the rock flakes or by beating upon the flakes until the lizards ran out. Some lizards were observed running about in the late afternoon in the shade of scant vegetation or in the shade of rock boulders (Roze, *personal communication*).

Distribution. *Phyllodactylus dixonii* is known only from the type locality. The type locality is approximately 35 km NE of Puerto Carreno, Colombia, and 385 km (airline) south of San Juan de los Morros, Venezuela, the nearest locality of *P. ventralis* (fig. 6).

Seven specimens have been examined from the following locality:

VENEZUELA. *Bolivar*: mouth of Rio Parguaza, on the Rio Orinoco MCNC 5479-80, MBUCV III 8451-54, TCWC 23827.

***Phyllodactylus sentosus* sp. nov.**

Phyllodactylus phacophorus, (part) Boulenger 1885, Cat. Lizards in the British Museum (Natural History) 2:84.

Holotype. Adult female, TCWC 27913. Collected by Fortunato Blancas, November 1949; Type locality, Lima, Department of Lima, Peru.

Definition. An average-sized gecko with maximum snout-vent length of 56 mm; large preanal plate absent; very large trihedral tubercles present on dorsum, forearm, thigh, tibia, and tail; ear denticulate on anterior and posterior margins; median row of scales beneath tail with few scales slightly enlarged, rounded; tail 45 to 50 per cent of total length; terminal lamellae of digits separated along median line, small, claw visible between and beyond tip of terminal lamellae when viewed from below (fig. 12a).

Diagnosis. This species may be distinguished from all other western South American species except *P. kofordi*, by the presence of very large tubercles on dorsum, thigh, tibia, forearm, and tail. *Phyllodactylus sentosus* differs from *kofordi* by having very small terminal lamellae on the digits and generally uniform sized scales beneath ventral surface of tail, rather than terminal lamellae large and all scales of median row beneath tail enlarged, rectangular.

Description of holotype. Rostral completely divided by vertical groove, twice as wide as high, its dorsal and lateral edges straight; two internasals, somewhat rounded, their median edges in narrow contact, bordered posteriorly by four granules and supranasal of each side; nostril surrounded by rostral, labial, supranasal, and one postnasal; first supralabial in narrow contact with ventral edge of nostril; no depression between internasals, slight depression in frontal region; 9 scales between eye and nostril, scales in posterior loreal region about three to four times larger than scales in midorbital region; 18 scales across snout at level of third labials, 12 scales across head between anterior edge of eyes, 14 midorbital scales; eye large, its diameter contained in snout length 1.7 times; eyelid with one to two rows of granules and one larger outer row of scales, last four to five are pointed; ear diameter contained in eye diameter 2.3 times; ear opening denticulate, scales on anterior and posterior margins pointed; rear of head granular with many larger intermixed tubercles; six supralabials and five infralabials to a point below center of eye; mental bell-shaped, slightly longer than wide, bordered posteriorly by three postmentals; postmentals rounded, slightly longer than wide, their median edges in broad contact, followed by transverse row of eight small scales, followed by second row of 11 smaller scales; postmentals contact first labial.

Dorsum with 16 longitudinal rows of enlarged, trihedral tubercles, paravertebral row with 26 tubercles from rear of head to base of tail, 13 between axilla and groin; paravertebral rows separated from each other by three rows of granules; 10 rows of tubercles reach to rear of head, 8 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by one to two granules; postanal tubercles number three on each side;

venter with 18 longitudinal and 48 transverse rows of scales; tail with 8 rows of tubercles in proximal eight whorls, distal one-third of tail regenerated.

Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among smaller flattened scales; dorsal surface of thigh with 8 to 9 tubercles interspersed among granular scales, tibia with 13 to 15 tubercles; lamellae formula for hand 6-8-12-11-8, foot 7-10-11-12-10; claw largely visible between and beyond tip of terminal lamellae when viewed from below; terminal lamellae small, about three times as long as wide.

Measurements in mm: Snout-vent length 50.0; axilla-groin length 25.0; leg length 19.3; arm length 16.0; tail length 46.3; head length 9.6; head height 7.8; head width 9.6; snout length 5.1; distance from eye to ear 4.6; eye diameter 3.0; ear diameter 1.3.

Color in alcohol: ground color fawn; dorsum with nine undulating crossbands of reddish brown, first two crossbands complete, remainder broken along midline of dorsum by cream middorsal stripe that begins about level of shoulder; each dorsal tubercle generally flecked with dark brown; limbs with brownish spots, forming faint reticulations on ground color; tail with six brown crossbands, about one-half width of ground color interspaces; distal one-third of tail regenerated; head brownish with wash of light brown; dark brown stripe from nostril to posterior edge of ear, bordered above by cream line on snout, above and below by cream line between eye and ear; ventral surfaces pale white, scales below tail with flecks of brown.

Variation. Snout-vent length of two males 49 and 56 mm (52.5); two females 39 and 50 mm (44.5); postmentals number two in three specimens, three in one; postmentals contact first labial only in all; number of scales across chin immediately following postmentals varies from 6 to 8 (7.3); number of scales bordering posterior edge of internasals vary from 5 to 7 (6.3), with internasals completely separated by an azygous scale in two of four specimens; scales across snout at level of third labial varies from 16 to 18 (16.5) midorbital scales vary from 13 to 14 (13.3); scales across venter vary from 18 to 21 (19.3); longitudinally 47 to 55 (50.3); number of enlarged rows of dorsal tubercles vary from 14 to 16 (15.0); number of paravertebral tubercles from rear of head to base of tail vary from 26 to 31 (28.8); from axilla to groin 13 to 16 (15.0); scales along line from nostril to eye vary from 9 to 10 (9.3); number of fourth toe lamellae vary from 12 to 13 (12.5); terminal lamellae of all digits very small, twice as long as wide; claw visible beyond tip of pad when viewed from below; number of enlarged rows of tubercles at base of tail number 8 in three specimens, 6 in one; 8 tubercles occur in each of 8 to 11 whorls on proximal two-thirds of tail, reducing rapidly in sequence to 6-4-2-0 on distal third of tail; median row of scales beneath tail generally uniform in size to other scales but occasionally a larger, rounded scale may be present.

Number of dorsal body bands varies from 8 to 10 (9.0), with majority of bands broken along midline of body in three specimens, bands loosely con-

nect and form reticulated pattern in one; tail bands number 13 and 14 in two specimens with complete tails; venter pale white to dirty cream; dark lateral face stripe continues to shoulder region as dashed line in two specimens, reaches to ear in two.

Comments. *Phyllodactylus sentosus* closely resembles *kofordi* (NW Peru), *darwini* (Galapagos Islands), *wirshingi* (Puerto Rico), and *martini* (Dutch Leeward Islands) in general appearance. The latter four species have enlarged trihedral tubercles on the dorsum, tail, thigh, tibia, and forearm. However, the four species have the median row of scales beneath the tail much enlarged and widened, and have moderately large, well defined terminal lamellae on all digits. In addition, *martini* and *wirshingi* have higher numbers of enlarged rows of dorsal tubercles (18 to 20) and higher numbers of paravertebral tubercles from head to base of tail (32 to 40). The number of enlarged dorsal rows of tubercles in *darwini* are identical with those of *sentosus*, but *darwini* has higher numbers of paravertebral tubercles from head to base of tail (33 to 38) and differs in several other features of squamation.

Natural history. The only known habitat of this species is the grounds surrounding the University of San Marcos in Lima. Dr. Gambini (*personal communication*) indicated that she found one specimen running across a sidewalk on the campus just after dark.

Distribution. Known from the University of San Marcos campus, Lima, Peru, and from the vicinity of the city (fig. 5). Six specimens have been examined: *Lima*: Lima BMNH 63.2.3.18-19, TCWC 27913, 28329-31.

Phyllodactylus reissi Peters

Phyllodactylus reissi Peters, W. 1862. Monatsb. Konigl. Akad. Wiss. Berlin, Nov., 1862, pp. 626-27.

Phyllodactylus baessleri Werner 1901. Abh. u. Ber. d.k. Zool. u. Anthr.-Ethn. Mus. zu Dresden, 9(2):2.

Phyllodactylus guayaquilensis Werner 1910. Mitt. Naturh. Mus. Hamburg, 27(2):4.

Phyllodactylus abrupteseriatus Werner 1912. Mitt. Naturh. Mus. Hamburg, 30:4.

Phyllodactylus magister Noble 1924. Occ. Pap. Boston Soc. Nat. Hist., 5:110.

Syntypes. Berlin Mus. 3734 (4), 4567 (2); BM 4567, ad. female, snout-vent 64 mm, herein selected as the Lectotype; Carl Reiss, collector; date of collection unknown. Type locality: Guayaquil, Ecuador.

Definition. A large gecko, maximum snout-vent length of 75 mm; femur tubercles absent, tibia tubercles present; ear strongly denticulate on anterior and posterior margins; enlarged tubercles on rear of head present; median row of scales beneath tail distinctly widened; enlarged preanal plate absent; 12 to 18 rows of enlarged trihedral tubercles on dorsum; tail about 48 to 58

per cent of total length, without whorls of enlarged tubercles; terminal lamellae of digits moderately enlarged, truncate; dorsal color pattern variable, uniform in color to bold bands; venter usually yellowish (fig. 13b).

Diagnosis. This species may be distinguished from *P. heterurus*, *angustidigitus*, and *gerrhopygus* by the absence of enlarged preanal plate; from *lepidopygus*, *microphyllus*, *clinatus*, and *inaequalis* by the presence of tibia tubercles and larger size; from *interandinus* by its larger size (average s-v of 58.3 mm rather than 40.1 mm), fewer number of head to tail tubercles in paravertebral row, 47 to 60 rather than 64 to 81; from *kofordi* by its larger size (as above) rather than average of 44.0 mm, and by having more head to tail tubercles in paravertebral row (as above) rather than 31 to 36; from *johnwrighti* and *pumilus* by larger size, a maximum snout-vent length of 75 mm rather than 51 mm; thigh tubercles absent, rather than present; from *sentosus* by absence of tail and forearm tubercles, larger scales in median row beneath tail, larger terminal lamellae, and color pattern.

Description. Rostral about twice as wide as high; internasals rounded, their median edges in broad contact, bordered posteriorly by small granules and postnasal of each side; nostril surrounded by rostral, labial, internasal, and two postnasals; first labial in broad contact with ventral edge of nostril; shallow depression between internasals, deep depression in frontal region; scales in posterior loreal region about 3 to 4 times larger than midorbital scales; eye large, its diameter contained in snout length about 1.8 times; eyelid with 2 rows of granules and 1 larger outer row of scales, last 3 to 6 of which are pointed; diameter of ear contained in eye diameter about 2.1 times; ear opening strongly denticulate with pointed scales on the anterior and posterior margins; rear of head granular with larger intermixed tubercles; 6 to 7 supralabials and 5 to 6 infralabials to a point below center of eye; mental bell shaped, as wide as long, bordered posteriorly by two to four postmentals; postmentals slightly longer than wide, their median edges in broad contact.

Dorsum with longitudinal rows of enlarged trihedral tubercles that are somewhat elevated; paravertebral rows separated from each other by 4 to 5 rows of granules; 6 rows of tubercles reach to nape, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 0 to 2 granules; postanal tubercles number 4 on each side, distinct and slightly elevated posteriorly in males; dorsal surface of upperarm with flattened scales, forearm with slightly larger flattened scales; dorsal surface of thigh without tubercles intermixed among smaller flattened scales; tibia with large tubercles scattered among granular scales; claw slightly visible when viewed from below; terminal pad large, slightly longer than wide, somewhat truncate at tip.

Variation. Snout-vent length of subadult and adult males range from 42 to 75 mm (59.4), females from 37 to 73 mm (57.5), juveniles from 22 to 35 mm (28.9), and males plus females average 58.3 mm; 48 per cent of total sample (753 specimens) were 60 mm or more in snout-vent length; postmentals vary from two to four, two occurring 97.4 per cent of the time, three

1.9 per cent and four 0.7 per cent; postmentals contact the first labial only in 96.8 per cent of sample, first and second labials 3.2 per cent; number of scales immediately following postmentals across chin vary from 5 to 8 (6.3); scales across midorbital region vary from 16 to 24 (20.2); scales across snout at level of third labial vary from 18 to 27 (23.7); scales bordering internasals posteriorly vary from 5 to 9 (6.7) with an azygous scale separating the internasals in 23.1 per cent of sample; transverse rows of scales across venter vary from 24 to 37 (29.7), longitudinally 54 to 77 (60.0); dorsal tubercular rows vary from 12 to 18 (13.2); paravertebral tubercles from head to tail vary from 47 to 60 (53.0); between axilla and groin 25 to 38 (31.3); scales along a line between nostril and eye vary from 10 to 16 (12.5); lamellae beneath fourth toe vary from 11 to 17 (13.5).

Dorsal color pattern highly variable, ranging from uniform yellowish tan without darker markings to light gray ground color with bold black undulating crossbands half the width of ground color interspaces; those with dark dorsal markings on ground color may have spots, crossbands, blotches, or lines that are either bold black, dark brown, brown, to indistinct grayish brown; in a few specimens the lines coalesce, forming a variegated pattern; when body markings are distinct enough to be counted, they generally vary from 5 to 7 pairs or single bands.

Coloration of dorsal surface of tail somewhat similar to that of dorsum; when bands are present they vary from 8 to 11 with 9 and 10 being most common; interspaces usually lighter than those of dorsum, tending to be more in contrast with darker bands; dorsal surface of head is either uniform in color, spotted or reticulated with dark brown to black lines or spots on ground color; side of head with or without distinct dark line from nostril through eye to arm; limbs similar to dorsum in color and pattern, with forearm and lower leg generally banded with dark on ground color in most specimens.

Ventral surfaces generally grayish white in alcohol (uniform pale yellow to tan with yellowish cast in life), with dark color of sides encroaching on venter in large individuals; ventral surface of tail usually darker than venter.

An examination of three populations of *P. reissi* from the coastal and coastal foothills of Ecuador, desert foothills surrounding the Sechura Desert of Peru, and the Marañon-Chinchipe Valley of northern Peru reveal very little variation in the majority of characters. The Ecuadoran population has an azygous scale separating the internasals in 43.1 per cent of the sample, 32.3 per cent in the Sechura Desert sample, and 14.3 per cent in the Marañon-Chinchipe sample. The number of enlarged dorsal tubercular rows vary from 12 to 16 (14 the common number), 12 to 16 (12 common), and 14 to 18 (16 common) respectively, in the three samples indicated above.

Comments. The types of *P. baessleri*, *abrupteseriatus*, and *quayaquilensis* were destroyed during World War II, but the characters mentioned in the

original descriptions of the latter two species fall within the variation present in *reissi*. An analysis of the characters of a large sample of *magister* from the *Marañon* and Chinchipe Valleys of Peru indicates only minor differences between it and populations of *reissi* from Ecuador and northern Peru. We, therefore, consider *abrupteseriatus*, *guayaquilensis*, and *magister* as subjective synonyms of *reissi*.

Werner's (1901) original description of *P. baessleri* is the only evidence we have for comparison of his species with those known to occur in Peru. His description does not correspond in its entirety to any population of *Phyllodactylus* we currently recognize in Peru. A translation of Werner's (1901, p. 2) original description follows:

"Closely related to *P. tuberculosus*, snout one and a half times as long as eye, somewhat longer than distance between eye and ear; frontal region with slight concave; ear opening diagonal, small diameter of ear one half that of eye; snout with large flattened, rounded scales, those of the rear of the head smaller, here they seem to differ by being mixed with small rounded tubercles; ear opening with three pointed scales on the anterior margin; rostral four-sided, the posterior margin with a short median notch; nostril surrounded by first labial and three nasals, of which the upper one contacts the upper nasal of the other side; 7-8 upper labials, 6th below eye; 7 infralabials; mental large, bell-shaped, followed by two small polygonal postmentals in contact with each other; followed by successively smaller scales in size; upper side of rump with 12 rows of strongly keeled tubercles, tubercles of each row close together; the two outer rows near the venter do not reach the forelimb; venter scales flat, overlapping, cycloid-hexagonal; tibia with enlarged keeled tubercles on the upper side; finger and toe ending with strongly enlarged lamellae, similar to *P. tuberculosus*; 4th toe with 16 lamellae, of which the distal one and mostly proximal ones are divided.

Color above, light grayish brown with black spots on head, tail, base of tail and legs; four long, black, parallel lines, from rear of eye to base of foreleg, two from back of head to middle of back, between the limbs; underside whitish.

Total length 91 mm, most of tail regenerated (39 mm); The single example on hand (D 1780 M. Dr.) came from Chanchamayo. The species is named in honor of Prof. A. Baessler."

From Werner's description (1901), we may eliminate the Peruvian species without strongly keeled tubercles on the dorsum, i.e. *P. microphyllus*, *inaequalis*, *gerrhopygus*, *angustidigitus*, and *heterurus*. His description mentions the presence of tibial tubercles, therefore we may eliminate *clinatus*, *interandinus*, and *lepidopygus*. The remaining species, *reissi*, *johnwrighti*, *sentosus*, and *kofordi* agree in part with his original description.

The latter four species have denticulate scales on the anterior and posterior margins of the ear, tibia tubercles, and strongly keeled dorsal tubercles.

Of these four species, only *P. reissi* has a fourth toe lamellae count (12 to 17) that falls within the range given by Werner for *baessleri*. Occasionally, *P. interandinus* has a few small tubercles on the tibia.

The color description given by Werner (1901) does not agree with any species of *Phyllodactylus* in Peru, while all other features mentioned in his original description agree with most of the species.

Werner's type locality, Chanchamayo, is also questionable. Chanchamayo is a well known, tropical lowland locality at the headwaters of the Rio Perene on the east side of the Andes. There are no known species of *Phyllodactylus* inhabiting the selva of eastern Peru.

We provisionally place *P. baessleri* as a subjective synonym of *reissi*, based upon the destruction of the holotype, a possible error in the type locality, and discrepancies in the original description when compared with known species in Peru.

Habitat and natural history. *Phyllodactylus reissi* is the most abundant scansorial gecko of northern Peru. Daytime retreats consist of any object that affords protection from predators and adverse temperatures. Individuals were found beneath bark of living, dead, standing, or prone trees, fence posts, fallen banana plants, standing and prone cacti, cracks in adobe walls, crevices in boulders, knot holes in trees, beneath bridges, rotting tree stumps, beneath palm leaves, construction materials and fruit crates. Their nocturnal activities were essentially on vertical surfaces, i.e., trunks of trees, walls of buildings, boulders, cacti, and fence posts, but occasionally were found actively foraging on the ground. Several were found foraging on open ground two to three meters from large boulders and in leaf litter in cacao groves.

This species is always found in association with some type of plant cover.

When exposed to daylight, *P. reissi* actively seeks a dark place to hide. When exposed in its daytime retreat, it hesitates only a few seconds before rapidly moving to another dark retreat. Its movements are usually vertical, but on horizontal limbs or tree trunks *reissi* usually runs to the ventral surfaces.

Two eggs are laid and usually deposited in rotting debris at the base of trees, beneath leaf litter in forests, in rotting agave stumps, hollow branches of dead cacti filled with debris, or in any rotting debris associated with its general habitat.

Phyllodactylus reissi has been found occupying the same cactus plant with *interandinus* in the upper Amazon Basin, and with *kofordi* in northwestern Peru. It has been found on the same tree with *Pseudogonatodes barboursi* and *Gonatodes atricucullaris*, and in the same general habitat with *inaequalis*, *clinatus*, and *microphyllus*.

As in all of the species of *Phyllodactylus* found in Peru, the nocturnal body temperatures of *reissi* closely approximated that of the substratum upon which it was active.

Distribution. This species is found from sea level to about 2,000 m in southern Ecuador and northwestern Peru. Its principal habitat seems to be

arid tropical scrub west of the Andes, and cacti dominated areas of the northern interandean basins of Peru (fig. 5).

Specimens (772) have been examined from the following localities:

ECUADOR. *Azuay*: 4 km E San Francisco USNM 167183 (23). *El Oro*: Machacha USNM 167182. Santa Rosa AMNH 22068. *Guayas*: Ancon Camp BMNH 1931.10.21.1-2. 6 km SW Colonche USNM 167189. Daule River MCZ 4740 (2). Guayaquil AMNH 21845. ANSP 7526. BM 3734 (4), 4567 (2). CMF 16504, 16540-46, 16658-61, 16676, 16695, 16700, 16850-51, 16889-900. EPN 4618 (18). FMNH 61210. HM 3386. Playas MVZ 77217-20, 77268. USNM 167181. Poza Huancauilca CMF 16512, 16515. Puente Chimbo AMNH 24343. Puna CAS 84770. 1 km NW Punta Cornero USNM 167190 (6). 0.5 km N Punta Cornero USNM 167191 (10). Salinas CMF 16531. *Loja*: BMNH 1930.10.12.13. Rio Casanga AMNH 18304-05. *Manabi*: Manta CMF 16522; FMNH 53896-98. 1 km S Manta USNM 167186 (5). 6 km E Manta, 5 km W Montecristi USNM 167188 (8). No specific locality in Ecuador AMNH 64569 (4); ANSP 7530; USNM 14052-53.

PERU. *Amazonas*: 14 km S Bagua Chica TCWC 28259. 17 km S Bagua Chica LACM 48766-72, TCWC 28260-64. 19 km S Bagua Chica LACM 48739-58, 48786; TCWC 28228-49. 10 km WSW Bagua Grande MVZ 82301. 8 km WSW Bagua Grande MVZ 82208, 82302-06. 15.5 km WSW Bagua Grande LACM 48759-64. TCWC 28250-55. 3.5 km SE Bagua Grande LACM 48765. TCWC 28256-58. *Cajamarca*: Bellavista AMNH 28525-27, 39339-40. FMNH 73379. LACM 48734-38. MCZ 42233 (3), 18126-29, 18141-42 (+ 208 unnumbered). TCWC 24923, 28210-21. UIMNH 41515, 40747. UMMZ 59029 (4). 4.8 km S Bellavista LACM 48734-38. TCWC 28222-27. Perico FMNH 100182-83. MCZ 17974, 18145-50. *Lambayeque*: 11 km N Jayanca MVZ 82197-201. 5 km SSW Motupe MVZ 82299. 7 km S Motupe LACM 48707-21, 48811-29. MVZ 82300; TCWC 28175-208. 15 km S Naupe MVZ 82202. 7.2 km W Naupe LACM 48773-74. TCWC 28265. 22 km E Olmos TCWC 28209. *Libertad*: Chiclin FMNH 34266. Pacasmayo HM (3 unnumbered); SMFM 8285, 8289. USNM 167180. *Piura*: Bayovar FMNH 9798-802, 9804. 1 km S Bayovar (Cerro Illescas) MVZ 85308-09, 85316-28. 1.1 km E Bocana LACM 48810. TCWC 28278-79. 1 km N, 28 km E Cabo Blanco MVZ 82177, 82232, 82280. Capullana Point FMNH 41551. Catalinas FMNH 9816-17. Cerro Amotape MVZ 82169, 82173, 82195, 82217-18, 82238, 82241, 82282, 82285-95. 8 km S, 8.4 km ESE Chulucanas LACM 48775-81. TCWC 28266-71. 2.4 km SW Chulucanas LACM 48782, TCWC 28272-73. El Alto FMNH 41548, 41550. Fondo MVZ 82272-73. La Breita BMNH 1926.3.24.6. 5 km E Las Lomas MVZ 82219-20, 82297-98. 2 km NE Las Lomas MVZ 85310-15. 3 km ENE Las Lomas LACM 48802-09. TCWC 28297-304. 5 km E, 4.2 km NNE Lobitos LACM 48798-801. TCWC 28291-96. Monte Grande MVZ 82279. Negritos FMNH 8364-65, 8384. Parinas MVZ 82207, 82276-77. Punta Sal SMFM 41913. Sechura Desert CAS 92346. 40 km WNW Sullana LACM 48783-84; TCWC 28274-75. 4 mi W Suyo

TCWC 24072-91. Talara AMNH 66600-01; FMNH 41547, 41549, 53895, 53892-93, 57456. 1 km SW Talara MVZ 82275. 2 km E Talara LACM 48785; TCWC 28276-77. Tamboa AMNH 28426-27. Tric Trac MVZ 85307. between Verdun Alto and Negritos FMNH 41546. *Tumbes*: Las Vocas USNM 38569. 1.2 km S, 1 km E Puerto Pizzaro LACM 48792-97; TCWC 28285-90. Quebrada Seca FMNH 9809, 9811-12; LACM 48787-91; TCWC 28280-84. no specific locality in Peru ANSP 13121; FMNH 41552-53; SMFM 8290.

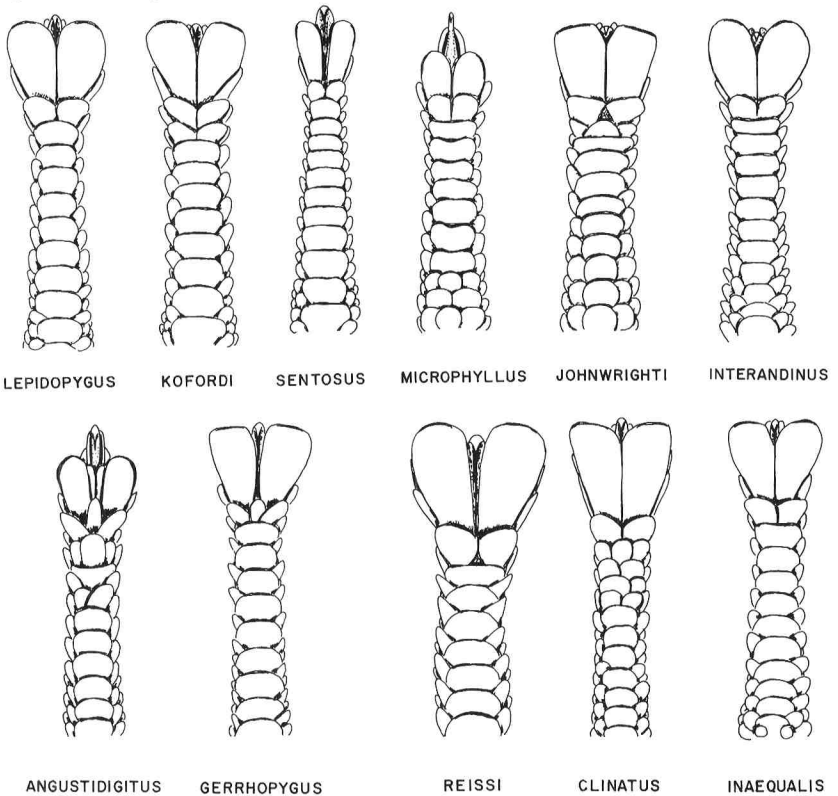


Figure 7. Ventral view of the fourth toe of all species of *Phyllodactylus* (except *heterurus* and *pumilis*) found on the mainland of western South America.

***Phyllodactylus johnwrighti* sp. nov.**

Phyllodactylus phacophorus, (part) Noble 1924, Occ. Paps. Boston Soc. Nat. Hist., 5:111.

Holotype. Adult male, TCWC 27916, collected by James R. Dixon and John W. Wright, 28 November 1968. Type locality. 13 km SSE (by road) Hacienda Molino Viejo, 1190 m, Department of Cajamarca, Peru.

Definition. A small gecko with a known maximum snout-vent length of 50 mm; enlarged preanal shield absent; dorsum and tibia with tubercles, absent from thigh, forearm, and tail; some scales of median row beneath tail widened and rounded; tail length about 49 per cent of total length; terminal lamellae moderately enlarged, rectangular; dark stripe from nostril to arm insertion always present (fig. 10b).

Diagnosis. This species differs from *P. angustidigitus*, *gerrhopygus* and *heterurus* by the absence of enlarged preanal shield; from *interandinus* by absence of dorsal stripes, presence of tubercles on tibia, and maximum number of 49 tubercles in paravertebral row from head to tail, rather than minimum of 65 in *interandinus*; from *kofordi* and *sentosus* by absence of forearm, tail, and thigh tubercles; from *reissi* by smaller maximum size, 50 mm rather than 75 mm, and absence of wide, rectangular row of scales beneath tail; from *microphyllus* and *inaequalis* by presence of regular longitudinal rows of enlarged trihedral tubercles on dorsum, from *lepidopygus* and *clinatus* by presence of tibia tubercles; from *pumilus* by absence of tail tubercles and smaller supraorbital scales.

Description of holotype. Rostral rectangular, twice as wide as high, its dorsal edge with vertical groove one-half depth of rostral; two internasals, subrectangular, their median edges separated by two granules; internasals bordered by rostral, nostril, six granules and postnasal of each side; nostril surrounded by rostral, labial, internasal, and two postnasals; first labial in broad contact with ventral edge of nostril; slight depression between internasals and in frontal region; 10 scales between eye and nostril; scales in posterior loreal region about 2.5 times larger than midorbital scales; 22 scales across snout at level of third labial, 14 scales across anterior edge of orbits, 20 midorbital scales; eye large, its diameter contained in snout length 1.6 times; eyelid with two rows of granules and one larger outer row of scales, last three to four are pointed; ear diameter contained in eye diameter 2.4 times; ear opening slightly denticulate, scales on anterior and posterior margins small, rounded and subequal; rear of head granular with intermixed tubercles; six supralabials and five infralabials to point below center of eye; mental bell-shaped, as wide as long, bordered posteriorly by two postmentals; postmentals rounded, slightly larger than other chin scales, their median edges in broad contact; postmentals immediately followed by transverse row of 7 scales, followed by second row of 10 smaller scales; postmentals contact first labial only of each side.

Dorsum with 14 longitudinal rows of enlarged trihedral tubercles; 10 rows reach to nape, 6 to base of tail; paravertebral row of 45 tubercles from head to tail, 26 between axilla and groin; paravertebral rows of tubercles separated from each other by five rows of granules, each tubercle separated from preceding tubercle by one to two granules; postanal tubercles three on each side; 26 scales across venter, 55 from throat to vent; tail without tubercles, median row of scales beneath tail with every other scale distinctly

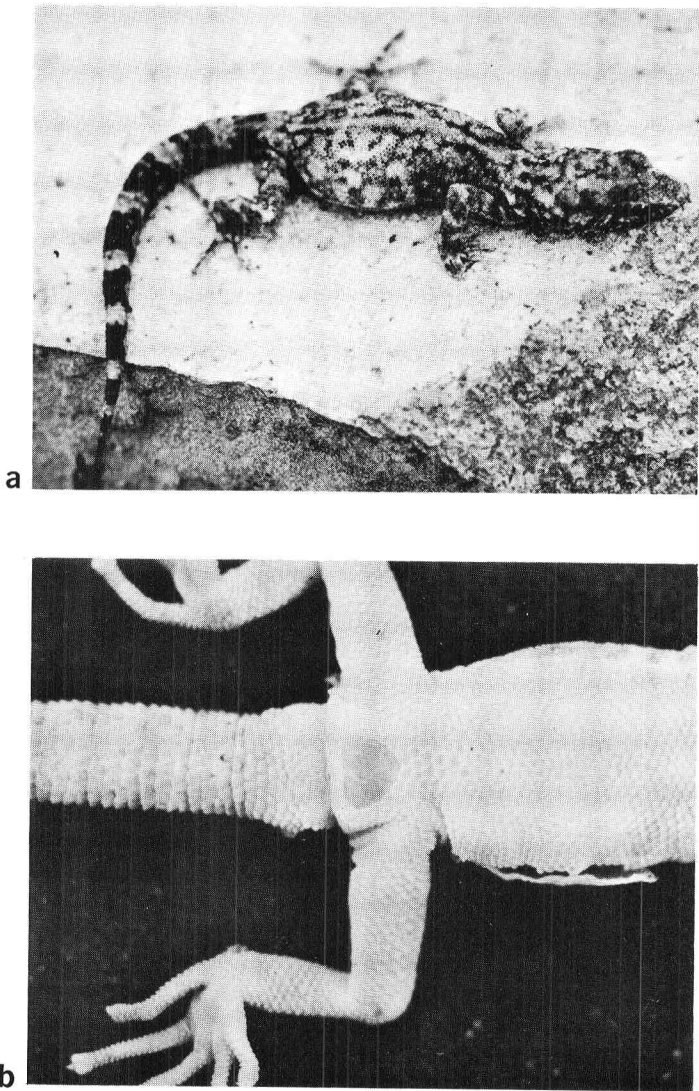


Figure 8. (a) dorsolateral view of *P. angustidigitus*; (b) ventral view of preanal plate of *P. angustidigitus*.

widened; arms and thigh with small flattened scales; thigh with five to six tubercles intermixed among scales; tibia with 17 to 19 tubercles intermixed among granules; lamellae formula for hand 6-8-9-10-8, foot 7-9-11-12-11; claw slightly visible when viewed from below; terminal lamellae large, rectangular, longer than wide.

Measurements in mm: Snout-vent length 39.0, axilla-groin length 17.4, leg length 14.8, arm length 11.8, tail length 34.0, head length 11.1, head depth 4.5, head width 7.6, snout length 4.2, eye diameter 2.7, ear diameter 1.1, distance from eye to ear 3.3.

Color in life: Ground color grayish tan; dorsum without distinct bands; grayish brown spots on anterior half of body, fading posteriorly; grayish yellow median stripe from nape to base of tail; posterior edge of scales on limbs stippled with dark brown, rest of scale ground color; head with diffuse spotting of grayish brown; grayish brown line from nostril to above arm insertion, bordered above by dirty cream line from nostril to ear; tail with 2 brownish black bands with yellowish brown interspaces; ventral surfaces dirty gray, with three to five black dots on each scale, more dense on tail.

Variation. Snout-vent lengths of subadult and adult males range from 32 to 40 mm (37.9), females from 33 to 44 mm (39.0), juveniles 21 to 31 mm (26.4), males plus females average 38.4 mm; tail length ranges from 46 to 51 per cent (48.8%) of total length; postmentals vary from two to four, three occurring twice and four once in 40 specimens; postmentals always contact first labial; number of scales immediately following postmentals vary from 5 to 8 (6.2); midorbital scales vary from 17 to 21 (18.8), scales across snout at level of third labials 20 to 26 (21.7); scales bordering internasals vary from 6 to 9 (7.5), internasals separated along median line by granules in 97.7 per cent of sample; scales from nostril to eye vary from 10 to 12 (11.1); scales across venter range from 26 to 32 (27.4), from throat to vent 47 to 57 (51.8); dorsal tubercular rows vary from 12 to 15 (13.9); paravertebral tubercles from head to base of tail range from 40 to 49 (45.0), between axilla and groin 22 to 29 (26.4); lamellae beneath fourth toe range from 10 to 12 (11.4); tubercles absent from tail.

Dorsal pattern generally uniform tan to pinkish tan, few individuals with double row of 9 to 12 small, grayish brown spots or transverse lines; tail usually banded with 11 to 16 black bands, with ground color interspaces of equal width; tail bands of juveniles usually bright orange and black, subadults yellowish orange and black, and adults yellowish brown and black; iris of eye pinkish gold, ventral surfaces generally dirty white in all specimens.

Comments. A distinct population of this species occurs on the east slope of the Andes at an elevation of 2100 m. One specimen of this population was taken by Noble from near the headwaters of the Rio Huancabamba in 1916, and three individuals were taken by us from near the summit of the Andes on the Olmos to Bagua road in 1968. These four specimens are similar in squamation to our series from near Molino Viejo, but differ in color pattern and

have a more decidedly depressed head and body. One male measured 50 mm and a female 46 mm in snout-vent length. The dorsal pattern consists of a fine reticulation of dark lines on ground color with a light median stripe. The lateral dark stripe extends from the nostril to midbody. Until additional specimens of this population are available, we are not in a position to analyze this population further.

This species is named in honor of Dr. John W. Wright, who discovered the original population along the Rio Huancabamba near Molino Viejo, and who provided us with an immeasurable amount of help in the field.

Habitat and natural history. This species occupies two distinct vegetation communities, the high, barren eastern slopes of the Andes where only a few cacti and shrubs are present, and a more extensive community of cacti, shrubs, mesquite, and broad leaved trees along the Rio Huancabamba and associated hillsides. The specimens from 2100 m were taken beneath dead *Cereus sp.* and a cholla-like cactus. Those along the Rio Huancabamba, taken during the day, were found beneath the bark of mesquite or under fallen trees. After dark, individuals were found emerging from beneath fallen *Cereus sp.* and from their branches as high as two meters above the ground. Later in the evening about 20 individuals were found foraging around the bases of small rocks, *Opuntia sp.*, weeds, and on open gravel soil. When disturbed, most individuals sought cover in small patches of weeds or among small rocks. Their nocturnal body temperatures averaged 23°C and closely approximated that of the substratum. Eggs of this species were found in rotting stumps of dead trees. An examination of the oviducts of preserved females indicates that this species lays one egg per clutch.

Distribution. This species has been found only on the arid slopes of the Rio Huancabamba Valley and higher barren slopes of the east side of the Andes in northwestern Peru (fig. 4).

Specimens (41) have been examined from the following localities.

PERU. *Cajamarca*: El Arenal MVZ 82196. 4.5 km W El Tambo TCWC 28088. 23.5 km WNW El Tambo TCWC 28104-05. 25.2 km WSW El Tambo TCWC 28106. 13 km SSE Molino Viejo LACM 48476, 48479-94, TCWC 27916, 28089-90, 28092-103. 11 km WNW Las Juntas LACM 48477-78, TCWC 28091. *Piura*: Huancabamba AMNH 28466.

***Phyllodactylus pumilus* sp. nov.**

Holotype. Adult male, USNM 167227, collected by James A. Peters, October 1965. Type locality. 1 km S Manta, Department of Manabi, sea level, Ecuador.

Definition. A small gecko with a known maximum snout-vent length of 51 mm; enlarged preanal shield absent; dorsum, tibia, and part of tail with tubercles; scales of median row beneath tail widened and rounded posteriorly; tail about 50 per cent of total length; scales in supraocular region largest of interorbital series; dark brown to black stripe from nostril to arm insertion

always present; terminal digital lamellae moderately enlarged and somewhat rectangular in shape (fig. 14c).

Diagnosis. This species differs from *P. angustidigitus*, *gerrhopygus*, and *heterurus* by absence of enlarged preanal shield; from *interandinus* by absence of dorsal stripes and presence of tubercles on tail and tibia; from *kofordi* and *sentosus* by absence of forearm tubercles and tubercles on distal two-thirds of tail; from *microphyllus* and *inaequalis* by presence of regular rows of enlarged trihedral tubercles on dorsum; from *lepidopygus* and *clinatus* by presence of tibia tubercles; from *reissi* by smaller maximum snout-vent length of 51 mm rather than 75 mm, scales in supraocular region largest of interorbital series, and at least two rows of enlarged, flattened scales on proximal one-fourth of tail; from *johnwrighti* by presence of at least two rows of enlarged, flattened scales on proximal one-fourth of tail; more transverse

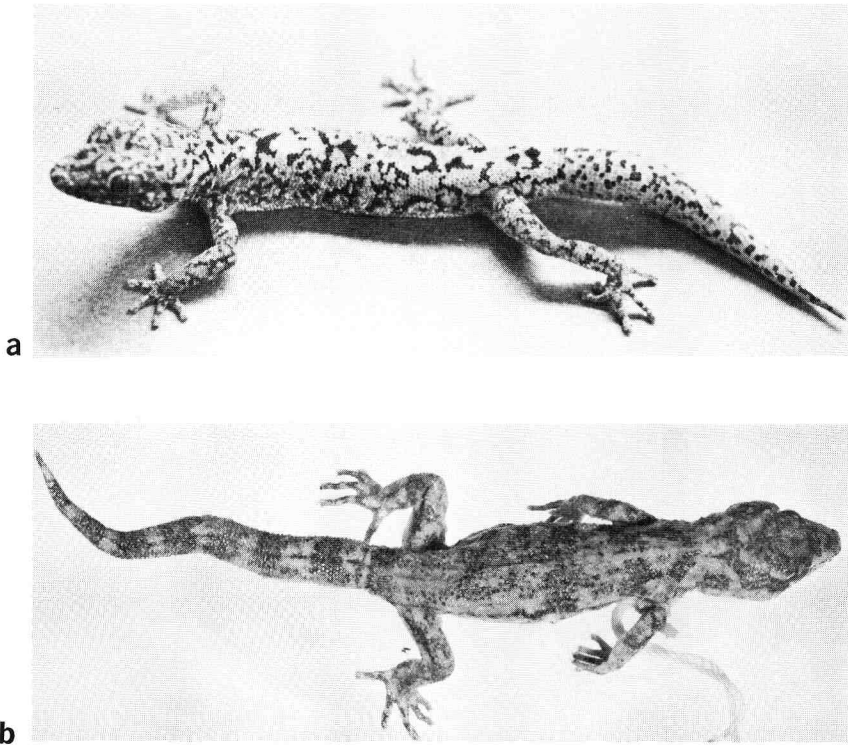


Figure 9. (a) dorsolateral view of *P. gerrhopygus*; (b) dorsal view of *P. microphyllus*.

ventral scales from throat to vent, 53 to 62 (57.6) rather than 47 to 57 (46.4); fewer paravertebral tubercles from head to base of tail, 37 to 43 (39.4) rather than 40 to 49 (45.0).

Description of holotype. Rostral twice as wide as high, its dorsal edge with short median, vertical groove; two internasals, somewhat rectangular and in contact along median edges; nostril surrounded by rostral, labial, internasal, and three postnasals; first supralabial in broad contact with ventral edge of nostril; shallow depression between internasals and in frontal region; 11 scales between nostril and eye; scales in posterior loreal region about three times larger than interorbital scales; 19 scales across snout at level of third labials, 17 interorbital scales, 18 at anterior edge of orbits; eye large, its diameter contained in snout length 1.7 times; eyelid (brille) with one to two rows of granules and one larger outer row of scales; diameter of ear contained in eye diameter about three times; ear opening strongly denticulate on anterior and posterior margins; rear of head granular with a few larger tubercles intermixed; six supralabials and five infralabials to point below center of eye; mental bell-shaped, as wide as long, bordered posteriorly by two postmentals; postmental about as long as wide, their median edges in broad contact; postmentals immediately followed by transverse row of six scales, followed by second row of 10 smaller scales; postmentals contact first labial only.

Dorsum with 14 longitudinal rows of enlarged trihedral tubercles that are somewhat flat; paravertebral row with 42 tubercles from rear of head to base of tail, 25 between axilla and groin; paravertebral rows separated from each other by four rows of granules; five rows of tubercles reach nape, six to base of tail; each tubercle of dorsal series separated from preceding tubercle by none to two granules; postanal tubercles number four to each side; venter with 27 longitudinal and 61 transverse rows of scales.

Dorsal surface of arm with large, flat scales; dorsal surface of thigh with three to five tubercles scattered among granular scales; lamellae formula for hand 7-8-9-9-7, foot 7-8-12-12-10; claw slightly visible when viewed from below; terminal lamellae slightly longer than wide, moderately enlarged; distal three-fourths of tail regenerated, proximal one-fourth with a 6-4-2 reduction in number of tubercles per whorl, decreasing in number towards distal portion of tail; median row of scales beneath tail widened, rounded posteriorly.

Measurements in mm: snout-vent length 49.0, axilla-groin length 22.0, leg length 17.5, arm length 12.5, tail length 44.5, head length 13.0, head width 9.3, head depth 5.7, snout length 5.2, eye diameter 3.0, ear diameter 1.1, eye to ear distance 3.7.

Color in alcohol: ground color grayish tan; dorsal surface of body with faint indication of six light brown bands, broken along median line of body by longitudinal stripe of ground color; limbs without pattern, ground color; top of head from occiput to snout uniform light brown; brownish stripe from nostril to arm insertion, passing over ear; supralabials spotted with dark brown,

less so on infralabials; venter grayish white with a few minute black dots on each scale; ventral surfaces of hands and feet slightly darker than venter; tail with faint indication of banding.

Variation. Snout-vent length of young adult and adult males range from 37 to 51 mm (44.0), females from 41 to 44 mm (42.0), juvenile 25 mm; males plus females average 43.2 mm; tail partly regenerated in all specimens except one and averages about 50 per cent of total length; two postmentals in all, contacting first labial only in 100 per cent of sample; number of scales immediately following postmentals vary from 4 to 8 (6.1); midorbital scales vary from 15 to 18 (16.9), scales across snout at level of third labial 19 to 22 (20.1); scales bordering internasals vary from 5 to 8 (6.0); internasals in contact along their median edges in 90.1 per cent of sample; scales between nostril and eye vary from 10 to 13 (11.6); scales across venter range from 27 to 30 (28.5), from throat to vent 53 to 62 (57.5); dorsal tubercular rows vary from 12 to 14 (13.3); paravertebral tubercles from head to base of tail range from 37 to 43 (39.4), between axilla and groin 23 to 27 (24.7); lamellae beneath fourth toe vary from 11 to 13 (12.0); at least two rows on enlarged, flat scales (may be elevated and tubercular-like) on proximal one-fourth of tail.

Dorsal color pattern highly variable, from an almost uniform light brown to definite paravertebral rows of dark brown spots or bands; head usually uniform light brown, but faintly mottled with light gray in some specimens; dark brown stripe from nostril to arm insertion in all but one specimen which has stripe continuing to groin region; median grayish stripe on dorsum in all specimens, but faintly interrupted by black reticulating lines in one; tail banded brown and gray in only specimen with complete, original tail; venter grayish white in all.

Habitat and natural history. Dr. James A. Peters (*personal communication*) states that the type locality is a vertical rocky cliff on the beach, just above the high tide zone, 1 km south of Manta. The cliff surface is somewhat rotten, crumbles easily, and contains numerous holes and crevices. Four specimens of *P. pumilus* were taken from beneath rocks or in crevices along the cliff face. Peters indicated that he had not seen other specimens of *Phyllodactylus* this close to the ocean at any other point on the Ecuadorian coast.

Peters indicated that all specimens of this species were taken during daylight hours. Other specimens were found beneath loose bark on trees and stumps in a semi-desert area with low scrubby vegetation, or in a transition, dry to subdry forest.

Phyllodactylus reissi were taken with *pumilus* from the stump of an old ceiba tree 6 km E of Manta, and at the type locality.

Distribution. This species has been taken west of the Cordillera de Balzar in the department of Manabi of Ecuador, from sea level to approximately 200 m (fig. 3).

Specimens (11) have been examined from the following localities: ECUADOR. *Manabi*: 8 km W Jipijapa USNM 167184. 1 km S Manta USNM

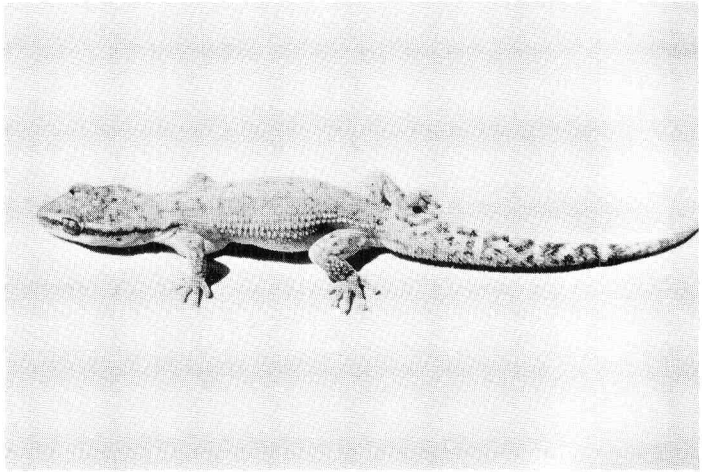
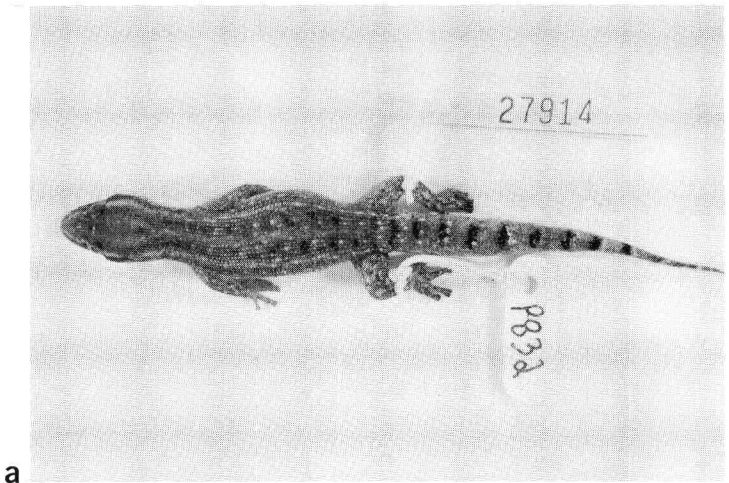


Figure 10. (a) dorsal view of *P. interandinus*; (b) dorsolateral view of *P. johnwrighti*.

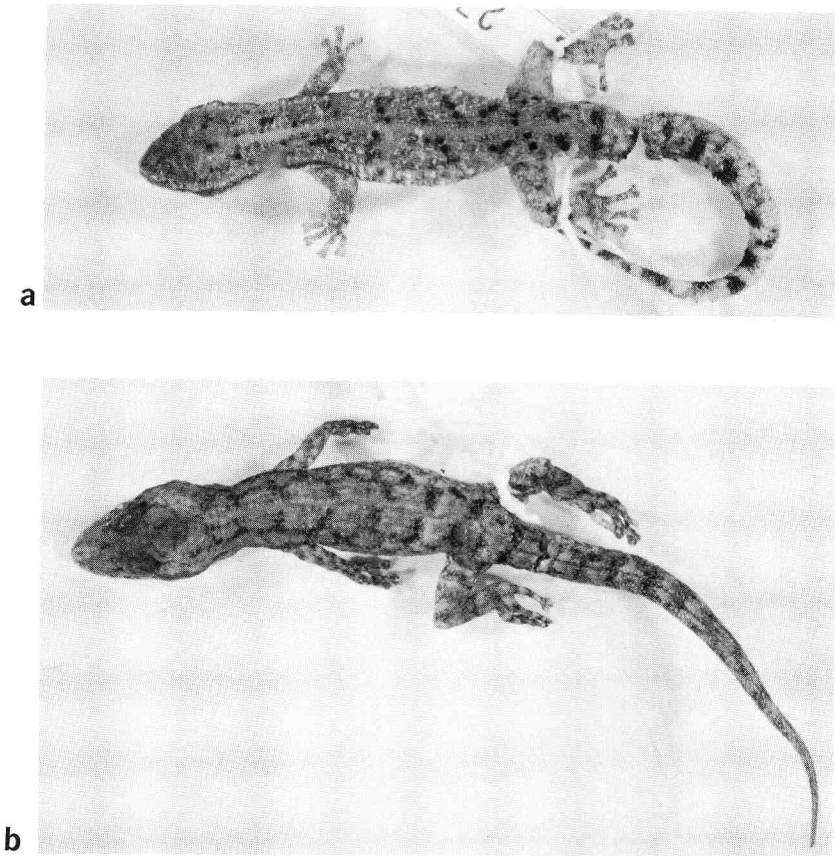


Figure 11. (a) dorsal view of *P. kofordi* (holotype); (b) dorsal view of *P. clinatus* (holotype).

167227-30. 6 km E Manta, 5 km W Montecristi USNM 167233. 11 km W Portoviejo USNM 167185, 167226. 9 km N San Vicente USNM 167187, 167231-32.

ADAPTATION TO HABITAT

Species of *Phyllodactylus* are, in the more restricted sense, geckos of arid and semiarid regions. Only on the mainland of British Honduras and some islands of the Caribbean are they found in a more tropical environment.

Adaptations of species of *Phyllodactylus* for living in arid deserts and

tropical deciduous forests are generally of two types, scansorial and terrestrial. Most of these lizards are found in areas where sufficient physical objects are available for scansorial habits, i.e. trees, rocks and cliffs. All species of Mexico, Central America, and eastern South America are scansorial. Most prefer a rock substratum, but are frequently found on trees and shrubs. Only on the mainland of western South America does one find a shift to the terrestrial habit, and even then the terrestrial species are occasionally scansorial.

Underwood (1954) indicates that the most primitive condition in geckos is one of terrestrial habits with simple, clawed digits. Adaptations to a scansorial habit involved the development of pilose, friction lamellae beneath the digits, and in some cases, beneath the tip of the tail. He also states that there has been a number of independent reversions to terrestrial habits with a loss or reduction in the size of the lamellae.

Of the 15 mainland species of western South America, four are terrestrial: *P. microphyllus*, *angustidigitus*, *gerrhopygus*, and *sentosus*. Of these four species, *microphyllus* has become well adapted to an open, deep sand habitat, through reduction in size of the terminal lamellae, shorter and more muscular limbs, and swollen scales about the nostril with the nasal opening a very small slit and lying in an anterior, dorsolateral position.

Phyllodactylus angustidigitus has become adapted to a shell and rubble beach habitat through reduction in the terminal lamellae, enlargement of the claw, elevated and swollen scales about the nostril, but unlike *microphyllus*, the limbs are very slender, long, and without much muscular development. Little is known about the habits of *sentosus*, but all known specimens were taken from the ground and they have relatively small terminal lamellae and well developed claws, but the region about the nostril is unswollen. We find it difficult to explain the presence of enlarged terminal lamellae in a terrestrial species, such as *gerrhopygus*. This species has very large, well developed terminal lamellae like those of scansorial species (fig. 7), but has the area about the nostril greatly swollen, and the limbs are intermediate in size and shape between *angustidigitus* and *microphyllus*.

There appears to be differential development for a terrestrial habit for each of the four species, with evolutionary trends variable within each population. For example, *P. microphyllus* taken from hard surface sands or conglomerate soils have slightly larger terminal lamellae than those from soft sands. However, in *gerrhopygus*, the size of the terminal lamellae varies slightly within each population and does not seem dependent upon soil type. The reduction in the size of the terminal lamellae coupled with an enlargement of the claw in *angustidigitus*, seems to be a special modification for living on shell and rubble beaches. Whether the reduction in the terminal lamellae and enlargement of claws are for walking on shell and rubble, or for turning over these objects in search of food is not known, but the claw is approximately four times the size of the claw of *gerrhopygus*, a species that is frequently found on sandy beaches.

The terminal lamellae of the scansorial species (*P. reissi*, *lepidopygus*, and probably *clinatus*) are generally greatly enlarged. *Phyllodactylus reissi* has exceptionally large toe pads, possibly influenced by its large body size. Several geckos are intermediate in their microhabitat preferences, *P. kofordi*, *inaequalis*, *johnwrighti*, and *interandinus*, usually spending the day under bark or exfoliations, and at night foraging about on the ground. As one might expect, the toe pads are intermediate in size, reflecting an adaptation to both terrestrial and scansorial habits. In addition, a toe pad of intermediate size may facilitate terrestrial locomotion over a broken substratum and surface debris typical of the habitats where these geckos are found. Seemingly, the more scansorial a species becomes, the more natural selection favors an enlargement of the terminal lamellae. However, this does not explain the enlarged terminal lamellae of *gerrhopygus*. This species has been taken from terrace walls and walls of houses indicating it is not completely terrestrial. There may have been a recent shift from a scansorial to a terrestrial habit, and natural selection for small terminal lamellae is presently acting upon the population. However, it is possible that *gerrhopygus* is adapted for running upon soft surface sand and foraging for surface food items. This would, in part, account for the small claws and enlarged terminal lamellae. Larger and more lengthened claws may be used for turning over surface litter or for digging under it in search of food (*microphyllus*, *sentosus*, *angustidigitus*). Large terminal lamellae would likely hinder the ability to dig or clasp objects in the search for food, whereas a surface feeder might retain the large lamellae, enabling it to move faster, farther, and with more ease, in search of surface food items.

The swollen area about the nostril seems to be an adaptation for living in regions where deep sand is constantly being moved about by wind action. The scales about the nostril are elevated, rounded (swollen), and the position of the nostril has been shifted to a more anterior, dorsolateral position. The nasal opening is narrow and partially protected by an anterior extension of the upper postnasal scale into the nasal aperture. In effect, the elevated and rounded scales surrounding the nostril form a tubular opening. This type of nostril provides adequate air passage and prevents sand from clogging the aperture while the individual rests in daytime retreats or forages about on the sand at night.

Phyllodactylus sentosus is the only representative of a terrestrial species that does not have a tubular condition about the nostril. The substratum where it lives is more of a conglomerate soil, and selection for a tubular nostril is not one of the critical adaptive features for survival. None of the scansorial species have tubular nostrils.

SYMPATRIC RELATIONS OF *PHYLLODACTYLUS* IN WESTERN SOUTH AMERICA

An awareness of sympatry is essential in overcoming the subjectivity of morphological taxonomy. This section will briefly document known cases of

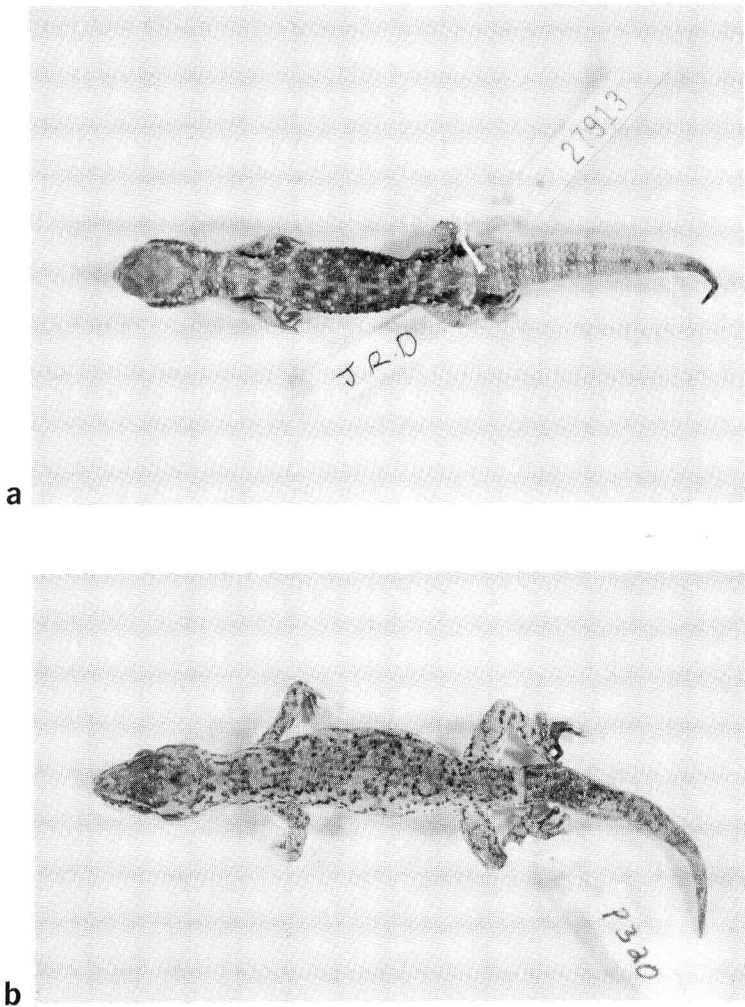


Figure 12. (a) dorsal view of *P. sentosus* (holotype); (b) dorsal view of *P. inaequalis*.

sympatry in western South America as well as describe certain aspects of ecological and evolutionary differences among the sympatric species.

The geographic distribution of species of *Phyllodactylus* is summarized in figs. 2-5. Known cases of sympatry are noted in Table 2.

When geckos occur sympatrically one consistently observes distinct differences in the degree of arboreality. For example, although both *P. reissi* and *interandinus* utilize arboreal perches for diurnal retreats, only *interandinus* moves to the ground for nocturnal foraging.

Phyllodactylus reissi and *kofordi* are commonly sympatric but have very little overlap in perch height. *Phyllodactylus reissi* is usually a scansorial forager, while *kofordi* is primarily a ground forager.

In some localities *P. inaequalis* is found with *kofordi* and *reissi* in sympatry. *Phyllodactylus inaequalis*, like *kofordi*, is a terrestrial forager. The relative abundance of these species seems to vary from locality to locality based on collecting records. It is not clear whether this is due to competition and/or to subtle environmental differences favoring one species at a given locality. There is some evidence of microhabitat separation between these two species at Cerro de la Vieja where *inaequalis* forages near the bases of boulders and *kofordi* forages more on open ground.

Another difference commonly found among sympatric geckos is in body size, presumably reflecting differences in prey size. In sympatric situations the only known exceptions to extreme body size differences are with *P. kofordi* and *inaequalis* as well as *kofordi* and *clinatus*. The fact that all of these geckos are small and appear to forage in different microhabitats probably accounts for their coexistence.

Some cases of sympatry are not clearly understood. The replacement of *P. microphyllus*, a sand gecko, by *kofordi*, normally a foothill gecko, along the sandy coast in extreme northwestern Peru is puzzling. Climatic, competitive, or physical environmental factors may be involved.

Selander and Giller (1963) observed that broad sympatry in woodpeckers of the genus *Centurus* occurs between distantly related species. Conversely, closely related species are allopatric or only narrowly sympatric. These workers concluded ". . . it is suggested that the evolution of reproductive isolating mechanisms tends to proceed more rapidly than does the evolution of ecologic isolation, with the result that competition and other interspecific interactions prevent extensive sympatry of closely related species . . ."

Pending completion of our osteological and karyological studies, the intrageneric relationships of the western South America *Phyllodactylus* are tentative. Strictly on the basis of external morphology, we suggest the following species are closely related and group them: *gerrhopygus*, *heterurus*, *angustidigitus*; *microphyllus*, *inaequalis*; *lepidopygus*, *clinatus*; *johnwrighti*, *pumilus*, *interandinus*; *sentosus*, *kofordi*; and *reissi*. Comparison of these groups with Table 2 shows only one known case of sympatry within a group, that of *gerrhopygus* and *heterurus*. However, the known extent of sympatry

TABLE 2

Sympatric relationships of 15 species of *Phyllodactylus* from the mainland of South America.

	<i>angustidigitus</i>	<i>clinatus</i>	<i>dixonii</i>	<i>gerrhopygus</i>	<i>heterurus</i>	<i>inaequalis</i>	<i>interandinus</i>	<i>johnwrighti</i>	<i>kofordi</i>	<i>lepidopygus</i>	<i>microphyllus</i>	<i>pumilus</i>	<i>reissi</i>	<i>sentosus</i>	<i>ventralis</i>	
<i>angustidigitus</i>																
<i>clinatus</i>						X		X		X			X			
<i>dixonii</i>																
<i>gerrhopygus</i>					X											
<i>heterurus</i>					X											
<i>inaequalis</i>		X						X						X		
<i>interandinus</i>														X		
<i>johnwrighti</i>																
<i>kofordi</i>		X				X					X		X			
<i>lepidopygus</i>											X					
<i>microphyllus</i>		X						X	X				X	X		
<i>pumilus</i>														X		
<i>reissi</i>		X				X	X	X		X	X					
<i>sentosus</i>											X					
<i>ventralis</i>																

(X = in sympatry)

of these species is based on one locality, and the status of *heterurus* is in doubt. Where broad sympatry does occur (e.g., among *inaequalis*, *kofordi*, and *reissi*), it is between or among very distinct species. Hence, Selander and Giller's (1963) conclusions might well be applicable to species of *Phyllodactylus* in South America.

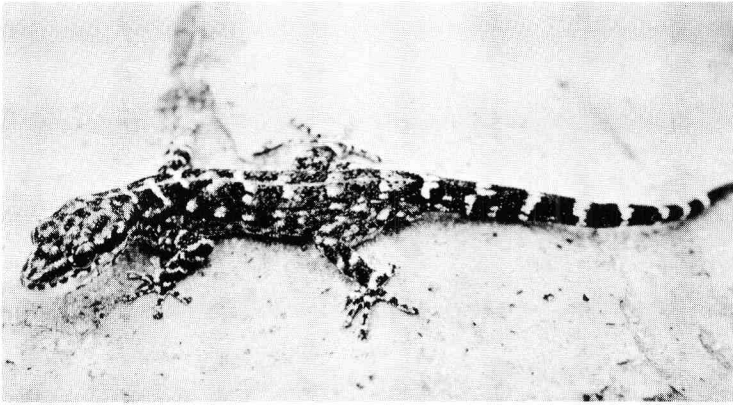
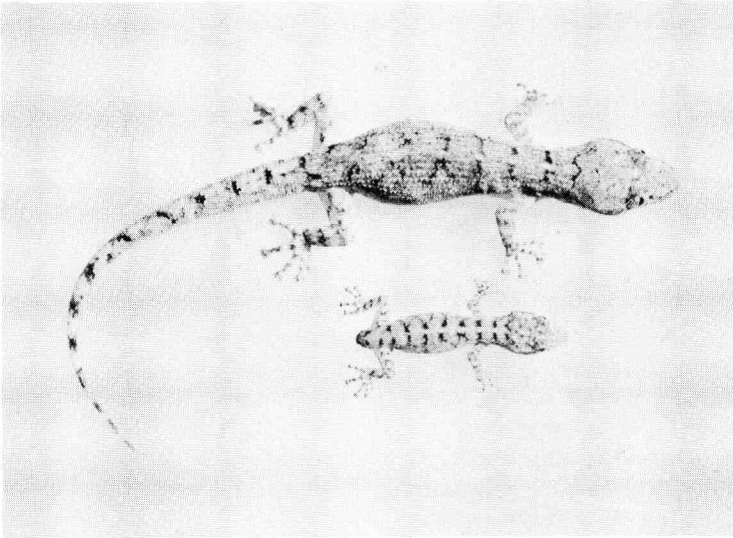
**a****b**

Figure 13. (a) dorsolateral view of *P. lepidopygus*; (b) dorsal view of an adult and young of *P. reissi*.

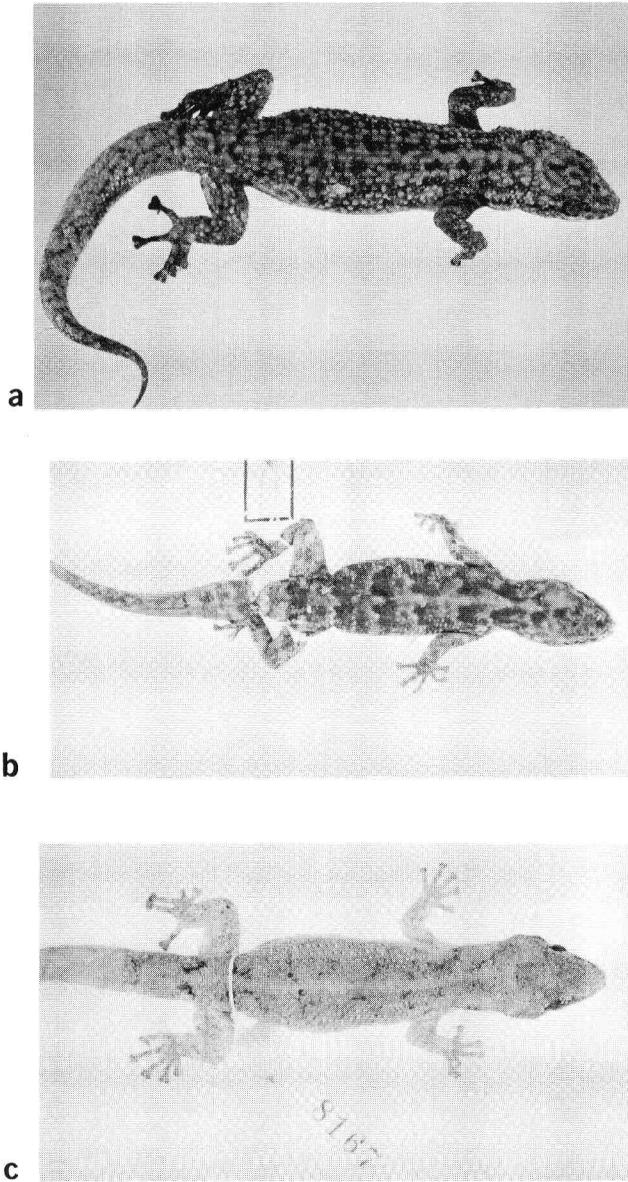


Figure 14. (a) dorsal view of *P. ventralis*; (b) dorsal view of *P. dixoni*; (c) dorsal view of *P. pumilus* (holotype).

GAZETTEER

There are a large number of collecting localities in Ecuador, Peru, and Chile not shown in gazetteers, on maps, or generally unavailable to scientists working with material from western South America. We present the following list of localities with coordinates, arranged by country and political division.

CHILE

Tarapaca

Arica	18° 29'S	70° 20'W
Iquique	20 13S	70 10W
Pica	20 30S	69 20W
Pintados	20 38S	69 38W
Pisagua	19 36S	70 13W
Putre	18 12S	69 35W

ECUADOR

Azuay

San Francisco	3 37S	79 30W
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El Oro

Machacha	3 16S	79 57W
Santa Rosa	3 27S	79 58W

Guayas

Ancon Camp	2 20S	80 52W
Colonche	2 01S	80 40W
Daule River	1 53S	79 58W
Guayaquil	2 10S	79 52W
Playas	2 38S	80 23W

Puente de Chimbo	2 11S	79 07W
Puna	2 42S	79 55W

Punta Cornero	2 18S	80 55W
Salinas	2 13S	80 50W

Loja

Loja	4 00S	79 13W
Rio Casanga	4 08S	79 49W

Manabi

Jipijapa	1 20S	80 35W
Manta	0 57S	80 45W
Portoviejo	1 03S	80 27W
San Vicente	0 36S	80 24W

PERU

Amazonas

Bagua Chica	5 38S	78 35W
Bagua Grande	5 47S	78 26W
Marafion Valley	4 30S	78 27W

Ancash

Chimbote

Valley	9 07S	78 38W
Culebras	9 56S	78 14W
Pativilca	10 40S	77 48W

Arequipa

Arequipa	16 24S	71 32W
Camana	16 37S	72 42W
Chucarapi	17 04S	71 44W
La Joya	16 45S	71 52W
Mollendo	17 02S	72 01W
Tambo	17 06S	71 48W
Vitor	16 26S	71 49W
Yura	16 12S	71 42W

Cajamarca

Bellavista	5 37S	78 39W
Chinchipe Valley	5 28S	78 32W
El Arenal	5 56S	79 17W
El Tambo	5 46S	79 24W
Las Juntas	5 57S	79 14W
Molino Viejo	5 49S	79 23W
Perico	5 15S	78 45W

Ica

Ica	14 05S	75 44W
Isla Sangallan	13 50S	76 28W
Isla Viejas	14 17S	76 12W
Jaguay	13 23S	76 12W
Lagunillas Bay	13 54S	76 18W
Marcona	15 20S	75 10W
Paraca Bay	13 50S	76 16W
Paracas	13 48S	76 15W
Paracas Peninsula	13 48S	76 24W
Pozo Santo	13 54S	76 03W
Puerto Pischo (new)	13 47S	76 17W
San Juan Port	15 22S	75 12W

Junin

Chanchamayo	10 42S	75 08W
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<i>Lambayeque</i>					<i>Capullana</i>				
Chiclayo	6	46S	79	51W	Point	4	29S	81	17W
Eten	6	54S	79	53W	Catalinas	4	11S	80	58W
Jayanca	6	24S	79	51W	Cerro Amotape	4	40S	80	58W
Mocupe	7	00S	79	37W	Chongollapi	5	26S	79	37W
Morrope	6	32S	80	02W	Chulucanas	5	06S	80	10W
Motupe	6	09S	79	43W	El Alto	4	17S	81	12W
Naupe	5	37S	79	54W	Fondo	4	28S	81	09W
Olmos	6	00S	79	45W	Huancabamba	5	14S	79	27W
<i>Libertad</i>					<i>Isla Lobos de</i>				
Chiclín	7	50S	79	10W	Afuera	6	57S	80	42W
<i>Jequetepeque</i>					<i>Isla Lobos de</i>				
Valley	7	21S	79	36W	Tierra	6	27S	80	52W
Pacanguilla	7	10S	79	28W	Las Lomas	4	40S	80	15W
Pacasmayo	7	24S	79	34W	Lobitos	4	26S	81	16W
<i>Lima</i>					<i>Los Organos</i>				
Ancon	11	46S	77	10W	Monte Grande	4	27S	81	02W
Asia	12	47S	76	35W	Negritos	4	38S	81	19W
Cerro Azul	13	03S	76	30W	Paita	5	06S	81	07W
Chorillos	10	46S	77	46W	Parinas Valley	4	30S	81	06W
Chosica	11	54S	76	42W	Piura	5	11S	80	38W
<i>Cruz de</i>					<i>Punta Aguja</i>				
Hueso	12	23S	76	46W	Punta Sal	5	51S	80	56W
<i>Isla San</i>					<i>Reventazon</i>				
Lorenzo	12	05S	77	15W	Sechura	5	34S	80	50W
Lima	12	03S	77	03W	Sechura Desert	5	50S	80	40W
<i>Lomas de</i>					<i>Sullana</i>				
Lechay	11	27S	77	18W	Talara	4	34S	81	17W
San Antonio	12	37S	76	37W	Tric Trac	5	51S	81	00W
<i>Verrugas</i>					<i>Tumbes</i>				
Canyon	11	53S	76	32W	Cancas	4	00S	81	00W
<i>Piura</i>					<i>Las Vocas</i>				
Bayovar	5	50S	81	03W	Puerto Pizzaro	3	39S	80	24W
Bocana	4	41S	80	18W	Quebrada Seca	4	23S	81	14W
Cabo Blanco	4	15S	81	14W					

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RESUMEN

Se hace una breve descripción del hábitat natural de las especies de *Phyllodactylus* encontradas en el continente de América del Sur. El micro-hábitat natural de cada especie se describe hasta donde ha sido posible. Poca a ninguna información se aporta sobre el micro-hábitat de *P. heterurus*, *setosus* y *clinatus*. Cuatro especies, *P. angustidigitus*, *gerrhopygus*, *microphyllus* y *setosus* son primariamente terrestres y alopatricas en distribución. Diez especies, *P. clinatus*, *dixonii*, *inaequalis*, *interandinus*, *johnwrightii*, *kofordi*, *lepidopygus*, *pumilus*, *reissi* y *ventralis* son arborícolas y únicamente *johnwrightii*, *ventralis* y *dixonii* no viven simpátricamente con una o más de las otras especies arborícolas. En donde tres o más especies viven simpátricamente, las áreas utilizadas para reposar durante el día y para la obtención de alimento se sobreponen escasamente.

Con la excepción de *P. reissi*, la cual produce dos huevos, todas las especies de *Phyllodactylus* encontradas en América del Sur continental depositan un sólo huevo por nidada. La deposición de huevos en forma comunal parece ocurrir con frecuencia entre el mayor número de especies, incluyendo aquellas que viven simpátricamente: *P. interandinus* y *reissi*, y *kofordi* y *reissi*.

Las especies del género *Phyllodactylus* parecen tener adaptaciones específicas a sus micro-hábitats naturales. Aquellas especies que habitan áreas rocosas se caracterizan por la presencia de laminillas digitales terminales ensanchadas, cabeza y cuerpo comprimidos dorsoventralmente y ventanas de la nariz localizadas lateralmente; en el caso de especies que habitan un micro-habitat arenoso las laminillas digitales terminales son pequeñas, la cabeza y el cuerpo redondeados y las ventanas de la nariz son valvulares y estan localizadas dorsolateralmente; finalmente, las especies que viven en playas de concha tienen laminillas digitales con uñas alargadas, cabeza y cuerpo delgado y ventanas de la nariz con válvulas situadas dorsolateralmente. Dependiendo del grado en que el comportamiento es arborícola o terrestre algunas especies de *Phyllodactylus* poseen las adaptaciones descritas en forma intermedia.

Para cada especie, excepto *P. heterurus*, se incluye un mapa de distribución junto con fotografías; además, se presenta una lista de localidades importantes.

De los holotipos y sintipos de las especies descritas de América del Sur continental, existen diez (*dixonii*, *inaequalis*, *lepidopygus*, *magister*, *microphyllus*, *nigrofasciatus*, *phacophorus*, *pumilus*, *reissi*, y *ventralis*), ocho de los cuales han sido examinados.

Se describen siete nuevas especies (*angustidigitus*, *clinatus*, *interandinus*, *johnwrighti*, *kofordi*, *pumilus* y *setosus*); nueve nombres antiguos se relegan al sinonimio de otras especies (*abrupteseriatus*, *baessleri*, *guayaquilensis*, *lobensis*, *magister*, *nigrofasciatus*, *phacophorus*, *underwoodi*, *variegatus*).

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