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Concerning the Relationship of Certain Neotropical Gekkonid Lizard Genera, with Comments on the Microscopical Structure of Their Glandular Scales

BY

EDWARD H. TAYLOR and A. BYRON LEONARD

Department of Zoology, University of Kansas

ABSTRACT: The classification of the gekkonid lizards is reviewed briefly. The recent family classification of the gekkonid lizards by Garth Underwood is discussed and followed as far as Western Hemisphere groups are concerned. The absence of femoral pores in all endemic species of the Gekkonidae in the Western Hemisphere is reported. The genera *Peropus* and *Hemidactylus* are regarded as transported here by man. Specialized glandular scales on the posterior ventral and subfemoral regions are discussed and a preliminary microscopical study of the scales is offered. The name "escutcheon scales," proposed for these by Chapman Grant, is used. It is believed that these scutes may represent the ancestral type of the femoral and preanal pores.

For a considerable time the gekkonid lizards have been of much interest to the senior author who in his field exploration in various parts of the world has collected representatives of some eighty forms of these interesting saurians, several of which have been described as new. His recent review of the lizard fauna of Costa Rica has again opened the problem of the classification of the gekkonid lizards and he found it necessary to make a cursory review of those groups occurring in the Western Hemisphere, and to make an attempt to re-evaluate the rank of the groups represented.

In the latter half of the 19th century the gekkonid lizards were regarded as belonging to three families: the Uroplatidae, Eublepharidae and the Gekkonidae. This arrangement was used by Boulenger in his British Museum Catalogue and by Cope in his work on American Herpetology. It was likewise followed by a majority of the herpetologists of their time.

Fürbringer (1900) published a classification of the lizards recognizing three families. However he placed the Uroplatidae in a

"*gens*" different from the other two. The following year Gadow (1901) considered all the gekkonid lizards under the suborder Geckones placing them in a single family, Geckonidae, with three subfamilies—Uroplatinae, Eublepharinae, and Geckoninae. After a time there was a tendency on the part of herpetologists to follow this arrangement, but not without some variation. Thus Charles Camp (1923) in his scholarly contribution on classification, reviewed the Sauria, recognizing the Uroplatidae as a distinct family but treating the Eublepharidae with the Gekkonidae.

One of the troublesome groups formerly associated with the Gekkonidae is one comprising certain small Central and South American saurians including the genera *Sphaerodactylus, Gonatodes, Pseudogonatodes, Coleodactylus* and *Lepidoblepharis.* Moreover, one cause for this trouble was that certain forms in South Asia (of different relationship) were placed in the genus *Gonatodes* erroneously, so that one had in a single genus both amphicoelous and procoelous forms, thus rendering the character of the vertebrae useless for the separation of families.

G. K. Noble (1921) in his study of *Sphaerodactylus* and allied genera noted the characteristics of the group in Central and South America. He found it necessary to remove this group of genera from the Gekkonidae proper and associate it with the Eublepharidae. Moreover, he did not include amphicoelous Asiatic forms in *Gonatodes.* Werner (1912) already had referred *Lepidoblepharis* to the Eublepharidae. Noble was convinced that these genera of small saurians represented a natural group. Concerning the vertebrae he states, "The procoelous vertebrae have been developed in this series quite independently of similar changes in any other series." Despite numerous other differences he associated them with the Eublepharidae chiefly on the basis of this one character.

H. W. Parker (1926) treated this same group, adding to it another genus, *Coleodactylus.* He subscribed to the Gadow classification and all were placed in the Gekkonidae. The Zoological Record of 1926 did not use the family name Eublepharidae and it did not appear in the American Checklist of Stejneger and Barbour of 1923.

Smith and Taylor in their Mexican checklist (1946) reluctantly followed this usage although it was apparent to both authors that the arguments were equally as strong for the retention as for the abandonment of the family. Since they were not treating species

of the Uroplatidae the status of that family was not their immediate concern. As for the group delineated by Noble, his opinion as to their relationship was accepted. The group entered Mexican territory only in the southern part and two diminutive species of *Sphaerodactylus* were the only ones available to them in their collections.

To the senior author in his studies of the Costa Rican fauna, the group was more important since Costa Rica has representatives of three genera and several species and the general characteristics of the group were examined. It was noted that, aside from the procoelous vertebrae, the paired parietals, sternum characters, and the sternum-rib relationship pointed out by Noble, they lacked a voice mechanism. The "clutch" consisted of a single egg at one laying. Neither postanal sacs nor postanal bones were present in either sex. It was noted that the males and females had no femoral or preanal pores but that there were present in males a series of specialized glandular scales in the posterior region of the venter. In some species these also appeared in the femoral region, suggesting their possible analogy to the true femoral and preanal pores.

He began a hasty search of the literature to ascertain whether these characters had been described and was informed by his student, Mr. Peter Chrapliwy, of the description by Maj. Chapman Grant (1931) in a paper dealing with West Indian members of the genus *Sphaerodactylus*, and of the work by Noble and Klingel. Grant who seemingly was the first to mention them in literature had given the name of "escutcheon scales" to this group of glandular scales. Noble and Klingel seem to have been the first and perhaps the only subsequent workers to give consideration to these scales. Aside from noting the escutcheon scales on certain species they made a preliminary study of the microscopical structure (Noble and Klingel, 1932).

From the first we were convinced that the group unquestionably merited at least subfamily recognition and proposed to deal with it in this category. Shortly after, we received a paper by Garth Underwood (Nov., 1954) * dealing on an extensive scale with the anatomy and classification of the Gekkoes.

While it is somewhat futile to report our own proposals for the arrangement of the American gekkonid lizards, they were as follows:

* This paper was first received by us in May, 1955. A report on our study was presented by the senior author at the 1955 meeting of the American Society of Ichthyologists and Herpetologists at San Francisco in June.

ARRANGEMENT OF AMERICAN GEKKONIDS

Eublepharidae
  Eublepharinae (with preanal pores)
    Coleonyx
  Sphaerodactylinae (with specialized glandular scales in males uncertain in Pseudogonatodes and Coleodactylus)
    Gonatodes Fitzinger
    Sphaerodactylus Wagler
    Lepidoblepharis Peracca
    Pseudogonatodes Ruthven
    Coleodactylus Parker
Gekkonidae (without preanal or femoral pores)
    Bogertia Loveridge
    Briba Amaral
    Thecadactylus Cuvier
    Aristelligella Noble
    Tarentola Gray
    Homonota Gray
    Phyllopezus Peters
    Aristelliger Cope
    Discodactylus Titschack
    Gymnodactylus Spix
    Phyllodactylus Gray
    (nonendemic imported forms) femoral and/or preanal pores present
    Hemidactylus Cuvier
    Peropus Wiegmann

Underwood has arrived at his classification largely through a study of the eyelids and the structure of the eye itself, characters that we had not considered in our own work. He has not used this, however, to the exclusion of other important characters. One significant fact which we overlooked was that sexual dimorphism in color was a presumed universal characteristic of the group. We were, of course, aware that it occurred in certain species.

Underwood recognizes the superfamily Gekkonoidea and under it his arrangement of families is as follows:

Gekkonoidea
  Eublepharidae
  Sphaerodactylidae
  Gekkonidae
    Gekkoninae (including Uroplatidae auct.)
    Diplodactylinae

We are accepting Underwood's general arrangement of families for the Western Hemisphere. There remains considerable doubt as to the wisdom of placing the Uroplatidae in the subfamily Gekkoninae since in so doing numerous significant characters seemingly are disregarded.

Since Underwood restricted the genus *Gymnodactylus* to South America, of the endemic genera of American gekkoes only *Phyllodactylus* has representatives outside of the Western Hemisphere with femoral or preanal pores. Tarentola also with Old World representatives may have some special glandular scales such as occur in *Sphaerodactylidae.*

The specific function of preanal or femoral pores has not been satisfactorily explained. The pores when present are usually in males; however, in some groups they may appear in females or they may be absent in both sexes. Thus the pores are present in the males of the Eublepharidae but are absent in all endemic genera and species of the Gekkonidae in the Western Hemisphere. Thus it would appear that there is nothing that acts as general inhibitor for the development of pores save in the case of the Gekkonidae. Nor would it appear that the absence of pores has had any marked effect on the success of the forms.

Species of *Hemidactylus* and *Peropus* have lines of femoral or femoro-preanal pores but we suspect that these species have all been imported or if they have developed into new subspecific forms, this has happened since their importation by man.* Seemingly these forms thrive here with the pores present and the question of their importance in survival is unanswered. Certain species of *Hemidactylus* have been described in the Western Hemisphere that were presumed to be of endemic origin.

In the Sphaerodactylidae the males of the Central American forms all have a group of glandular scales (escutcheon scales) in the posterior region of the venter and many have this series continued along the underside of the femur sometimes to near the knee; and in at least one genus (*Gonatodes*) some of the postanal scales may be so modified. These scales are not distinctly modified in the females.

Where series have been available the number of these scales has varied somewhat, and in the case of *Lepidoblepharis xanthostigma* the variation is considerable. It was noted that the smaller

* One might conceive of a pair of eggs of the highly domestic *Hemidactylus* carried to this country from the Philippines. The resulting animals might, in a relatively short time, with brother-sister matings, produce a population showing differences from the original Asiatic population due to the stoppage of gene flow from an Asiatic source.

numbers were counted in young males, the largest numbers in old males. As an example, the senior author reports on a series of specimens from Limón, Costa Rica, in which 28 to 46 could be counted in a juvenile and young adults, while 60 to 110 occurred in larger and older specimens. It seemed probable that while the entire lot of scales is early differentiated all do not take on their adult characteristics until much later. Even in some of the largest, presumably oldest specimens some of the scales adjoining the escutcheon scales often exhibited areas lacking surface pigment. The femoral scales in this species may be in a single row with three or four scales or there may be two rows with five or six altogether. These are always widely separated from the ventral escutcheon.

In the genus *Sphaerodactylus* this differentiation between young and old is less obvious and the femoral series, if present, are contiguous with the escutcheon scales on the venter. This genus has two groups in Costa Rica one of which has the escutcheon on the posterior ventral region but lacks entirely the femoral glandular scales; the other group has them present. The number and arrangement varies from species to species. We did not find any evidence of postanal glandular scales in the genus.

Gonatodes fuscus differs from the other two genera in having a larger number of the scales in the escutcheon. The area extends forward nearly one third of the length of the body, and consists of approximately 200 scales, with about 50 similar scales on the under surface of each femur.

It seems probable that the character of these scales will serve to assist in distinguishing species—perhaps subgenera and genera—in the family Sphaerodactylidae, and should be described in detail for each form.

While we have at hand no specimens of *Pseudogonatodes* or *Coleodactylus*, we have made a superficial examination of specimens of *Pseudogonatodes* at the Agassiz Museum at Harvard College.* We did not find the scales present in what we identified as males on the basis of external characters. We have seen no specimens of *Coleodactylus*. Should the escutcheon be absent in one or both of these genera it should not lessen the importance of the character as helping define the family. However, the poreless genera of the Gekkonidae should be carefully examined for species with scales of the escutcheon type.

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* Our thanks are due to Mr. Arthur Loveridge for the privilege of examining this material.

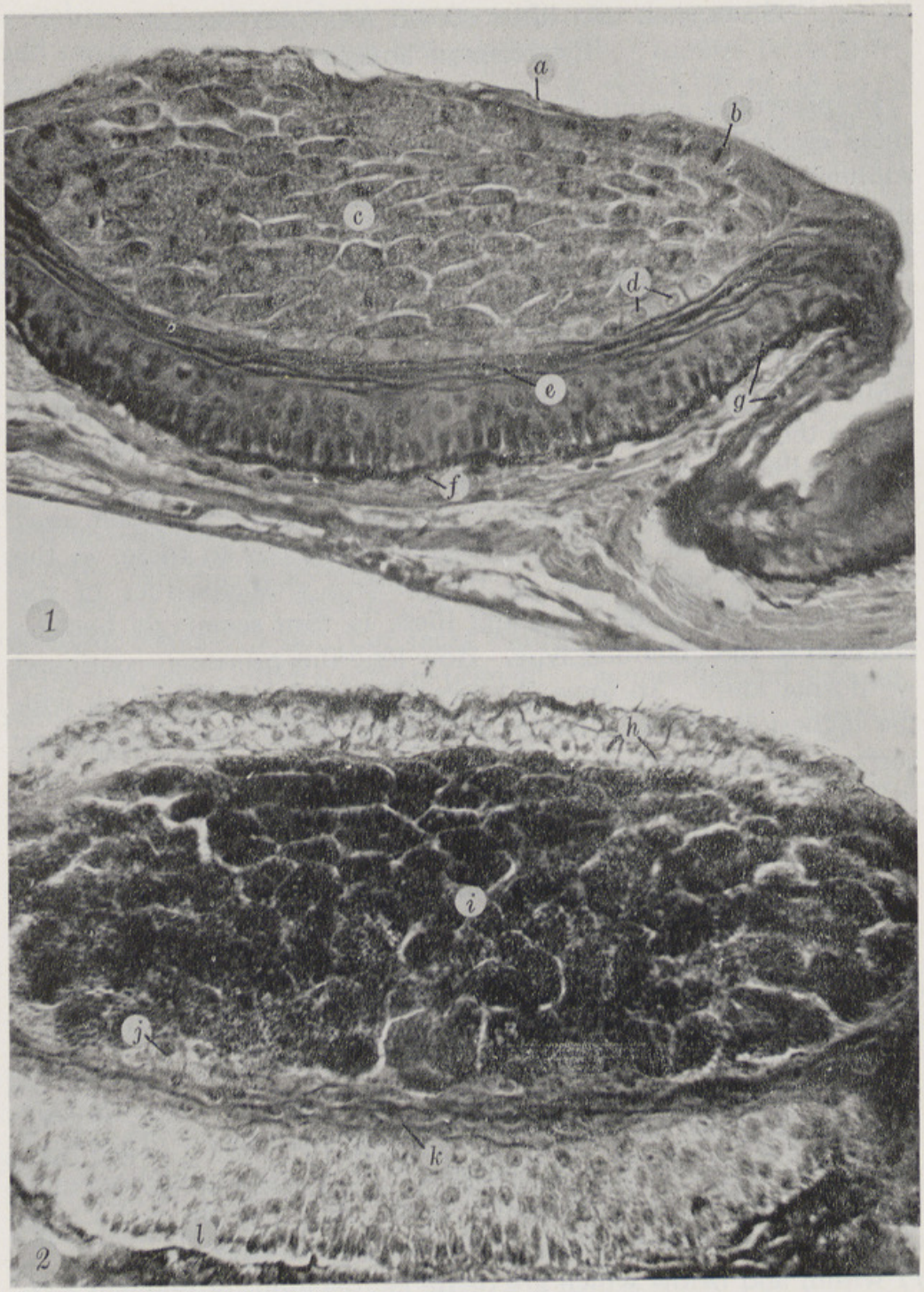
STRUCTURE AND MICROSCOPIC ANATOMY OF THE ESCUTCHEON SCALES

In preserved material the unpigmented surface epithelium of these escutcheon scales can be removed by gentle pressure and a rubbing movement of the thumb or finger. The normal scales, or the scales in the same area in females, remain completely intact by the same treatment. When the surface is removed the granular mass is exposed and may be partially or completely removed with a dissecting needle, thus leaving a cuplike depression lined by basal pigmented epithelium. Ordinarily the escutcheon cells are creamy white or white in color with a somewhat darker edge. This is due to the fact that the rim of the "cup" is pigmented and is visible through the transparent scale cover.

As pointed out the number of the visible glandular scales may be reduced in the young, but scales contiguous to these, as the animal grows older, take on the general characteristics of the glandular scales; scales touching these in turn seemingly become changed to the glandular type. How long this process is continued we do not know. In some old specimens of *Lepidoblepharis* with the highest numbers, adjoining scales may show a portion of their surface lacking pigment.

The histological specialization of the scales on the preanal, femoral, and sometimes the postanal regions of males of the Sphaerodactylidae is unique in our experience, and unlike any dermal specialization in lizards, or other animals, known to us.

The base of the scales in question is depressed to produce a definite pit, the floor of which is formed by a typical cornified stratified squamous epithelium and carries the typical pigmentation of *external* layers (fig. 1, *c*, *g*); this layer is continuous from scale to scale among the specialized ones, and continues onto the unspecialized scales, where it forms the superficial layer. This *basal epithelium* is typical of such epithelia as they occur in higher vertebrates generally; the germinative layer (fig. 1, *g*; fig. 2, *b*) rests on a basement membrane of collagenous connective tissue (fig. 1, *f*) within and below which are dense aggregations of pigment cells (fig. 1, *f*). Above the germinative layer, which consists of columnar cells for the most part, there is a layer of more or less rounded or polygonal cells ranging from three to eight cells in thickness. Near the surface of the basal epithelium the cells become flattened and cornified (fig. 1, *e*; fig. 2, *k*); it is these cells which on unspecialized scales form the outer protective desquamating covering.



Microscopic Anatomy of Specialized Scales from the Preanal Region of *Gonotodes fuscus* (Hallowell)

FIG. 1. *a*, cornified capping epithelium; *b*, germinative layer of capping epithelium; *c*, granular, "secretory" cells; *d*, germinative layer of "secretory" cells; *e*, cornified layers of basal epithelium; *f*, pigment cells below germinative layer of basal epithelium; *g*, continuity of basal epithelium from scale to scale. Celestine Blue and eosin; magnification, × 220.

FIG. 2. *h*, germinative layer of capping epithelium; *i*, granular cells of "secretory" epithelium; *j*, germinative cells of "secretory" epithelium; *k*, cornified layer of basal epithelium. Mallory's Triple Stain; magnification, × 250.

Within the depressed portions of the specialized scales, however, another germinative epithelium (fig. 1, *d*; fig. 2, *j*) composed of large faintly staining cuboidal to rounded cells lies in direct contact with the cornified cells of the basal epithelium. This second germinative epithelium produces large, polygonal to depressed rhomboidal cells containing dense accumulations of coarse granules (fig. 1, *c*; fig. 2, *i*) which are presumed to be secretory in nature. For this reason this layer is here referred to as the *"secretory" epithelium.* The cells of this layer fill the cuplike depression of the scale, and often produce a distinct convexity on the outermost surface. The granules of these cells stain faintly with Celestine Blue, but with Mallory's Triple Stain they become deeply pigmented (fig. 2, *i*). There is but little modification among these granular cells, except a slight degree of depression near the outer surface of the layer.

A third germinative epithelium rests on the granular cells of the secretory epithelium (fig. 1, *b*; fig. 2, *h*); these cells are cuboidal to rounded, and seem never to be columnar. They give rise to a layer not more than three to five cells in thickness which quickly becomes cornified and squamose; we refer to this outermost nonpigmented epithelium as the *capping epithelium.* This varies in thickness, but everywhere presents the same general characteristics and in preserved specimens as stated may be removed by rubbing a finger over the surface.

The arrangement of three distinctive superimposed epithelia in these scales not only provides a unique morphological feature that serves to distinguish these lizards from others known to us, but raises several intriguing biological problems. For example, how these superimposed epithelia are nourished, situated as they are above one or more layers of cornified cells of presumed impermeability, and certainly remote from the circulatory supply that lies below the basal epithelium, presents a difficult problem. Furthermore, the function of the secretory epithelium is unknown to us. It seems obvious that these cells pass through a cycle of biochemical stages, typical of secretory cells (compare fig. 1, *c* with fig. 2, *i*) since in our material it can be observed that the granules become larger as the cells enlarge; in addition, the staining properties of the cells when treated with Mallory's stain is not consistent; some cells stain deeply with fuchsin, others with aniline blue, and certain cells contain granules some of which take the blue stain, others the red. Still another problem is raised by the observation that the germinative layer of the secretory epithelium

and that of the capping epithelium are frequently out of phase; that is, when one seems active and well developed, the other seems less so (compare fig. 1 with fig. 2 with reference to the germinative layers). In some scales the capping layer seems to have desquamated to the point of nearly exposing the underlying secretory cells (fig. 1) but whether or not the secretory cells actually become exposed at the surface is not revealed by any of our material. Unfortunately for present purposes, all the material available to us was collected by the senior author in a single season (summer) of the year, so that presumed cyclic changes in the specialized scales cannot be determined at this time.

The relationship of these scales to the preanal and femoral pores is uncertain.* Their position on the body in the same general areas as the pores suggests that they may subserve the same general purpose. One might suspect that they represent a primitive stage in pore development. The femoral and preanal pores themselves are of several kinds and may be polyphyletic in origin. Further study is necessary to ascertain the degree of relationship.

LITERATURE CITED

BOULENGER, GEORGE A.

1885. Catalogue of the lizards in the British Museum (Natural History) 2nd ed. vol. 1, Geckonidae, Eublepharidae, Uroplatidae, Pygopodidae, Agamidae. 1885, pp. I-XII; 1-436, pls. 1-32.

CAMP, CHARLES LEWIS

1923. Classification of the lizards. Bull. Amer. Mus. Nat. Hist., vol. 48, art. XI, pp. 289-481, figs. 1-112.

FÜRBRINGER, M.

1900. Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. Jenaische Zeit., Bd. 34, pp. 215-718, pls. 13-17.

GADOW, HANS

1923. Amphibia and Reptilia (The Cambridge Natural History, vol. 8) 1923, pp. I-XII, 1-668, figs. 1-181.

GARDNER, LYNN W. and GRANT, CHAPMAN

1940. The herpetology of Jamaica, pt. 1, Amphibians; pt. 2, The Reptiles, Bull. Inst. Jamaica, Sci. Ser., no. 1, 1940, pp. 1-148.

GRANT, CHAPMAN

1931. The sphaerodactyls of Porto Rico, Culebra, and Mona Island. Jour. Dept. Agri. Porto Rico, vol. 15, no. 3, July, 1931, pp. 199-213, pls. 20-24 (first report on the "escutcheon" group of specialized scales).

* The preanal pores on the gekkoes of the genera *Naultinus, Hoplodactylus, Rachodactylus,* and perhaps others are arranged in patches or in several rows. The number is excessive and may reach 80 or more in one or more species. At the moment none of these lizards are available to us for examination. It is possible that these may throw some light on the relationship of the escutcheon scales to true femoral and preanal pores.

1932. A new sphaerodactyl from Porto Rico. Jour. Dept. Agri. Puerto Rico, vol. 16, no. 1, Jan. 1932, p. 31.

1936. Herpetological notes with new species from the American and British Virgin Islands. 1936. Jour. Agri. Univ. Puerto Rico, vol. 21, no. 4, Oct. 1937, pp. 503-522.

NOBLE, G. K.

1940. The bony structure and phyletic relations of *Sphaerodactylus* and allied lacertilian genera, with the description of a new genus. Amer. Mus. Novitates, no. 4, pp. 1-16.

1940. The herpetology of the Cayman Islands, Bull. Inst. Jamaica, Sci. Ser. no. 2, 1940, pp. 1-56.

Description of "escutcheon scales" in three species of *Sphaerodactylus*.

NOBLE, G. K., and HASSLER, W. G.

1933. Two new species of frogs; five new species and a new race of lizard from the Dominican Republic. Amer. Mus. Novitates, no. 652, Aug. 14, 1933, pp. 1-17.

NOBLE, G. K., and KLINGEL, G. C.

1932. The reptiles of Great Inagua Island, British West Indies. Amer. Mus. Novitates, no. 549, Aug. 11, 1932, pp. 1-25.

Discusses Grant's discovery of escutcheon scales and gives data on several species, and a brief description of their microscopic character.

PARKER, H. W.

1926. The neotropical lizards of the genera *Lepidoblepharis*, *Pseudogonatodes*, *Lathrogecko*, and *Sphaerodactylus*, with a description of a new genus. Ann. Mag. Nat. Hist., ser. 9, vol. 17, Mar. 1926, pp. 291-301.

SMITH, HOBART M., and TAYLOR, EDWARD H.

1950. An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. U. S. National Mus. Bull. 199, 1950, pp. I-IV, 1-253.

SMITH, MALCOLM

1933. Remarks on some Old World geckoes. Rec. Ind. Mus., vol. 35, pp. 9-19.

1935. The fauna of British India including Ceylon and Burma . . . Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. I-XII; 1-440, pl. 1, figs. 1-94.

TAYLOR, EDWARD HARRISON

1956. A review of the lizards of Costa Rica. Univ. Kansas Sci. Bull., vol. 38, pt. 1, pp. 1-322.

Treats of Sphaerodactylidae in Costa Rica.

WERNER, FRANZ

1912. Reptilia, Lacertilia (Eublepharidae, Uroplatidae, Pygopodidae). Das Tierreich, Lief. 33, pp. 1-33.