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# GEOGRAPHY OF THE SOUTH AMERICAN GEKKONIDAE (SAURIA)

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## INTRODUCTION

I have presented in this journal a check list of the geckos of continental South America and a review of the Brasilian species (Vanzolini, 1968). In the present paper I discuss the geography of the group, from the viewpoint both of the origin of the fauna and of its distribution within the continent.

Two well differentiated subfamilies of Gekkonidae occur in South America, the Sphaerodactylinae and the Gekkoninae (*sensu* Kluge, 1967). The Sphaerodactylinae are an entirely Neotropical group, a rather coherent and homogeneous one, whose more evident biological rationale is adaptation to diurnal life. Quite on the contrary, the South American Gekkoninae are a miscellaneous assemblage, with several diversified groups of genera, related to different Old World branches of the family. It is impossible to organize them in a single Neotropical or even New World scheme of evolution and distribution.

## THE GENERA OF SPHAERODACTYLINAE

Five genera are recognized among the sphaerodactylines: *Gonatodes, Lepidoblepharis, Pseudogonatodes, Coleodactylus* and *Sphaerodactylus*. Eight characters seem to me relevant to a discussion of their affinities.

1. *Pholidosis of the digits* (Vanzolini, 1968, figs. 1-5). *Gonatodes* has simple digits, not dilated, with the claw firmly ankylosed between one dorsal, two lateral, and one notched ventral scales; in the remaining genera the tip of the digits is modified into an ungual sheath. Noble (1921) was the first to establish a system of homologies of the sheath scales. Parker (1926) perfected the scheme, and I followed him (Vanzolini, 1957).

*Lepidoblepharis* has a symmetrical sheath, with the largest number (6) of differentiated scales; the mediodorsal series of unpaired scales is conserved, although the terminal one is small. In *Pseudogonatodes* the penultimate medio-dorsal element disappears, and the two laterals meet on the midline. In *Coleodactylus* (Vanzolini, 1957) the homologies are not very clear. There is a degree of hypertrophy of the la-

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teral half of the digit; the sheath is slightly gibbous, more so in *C. amazonicus* than in the remaining species. In *Sphaerodactylus* the sheath is disc-like, strongly asymmetrical, with a lateral slit for the claw. The infero-lateral scales are well differentiated, and one of the supero-laterals fused with the terminal. I do not believe that the sheath of *Coleodactylus* is ancestral to that of *Sphaerodactylus.*

2. *Inter-vertebral articulations. Gonatodes* has amphicoelous vertebrae. All other sphaerodactylines are procoelous.

3. *Shoulder-girdle.* The species of *Gonatodes* for which the character is known have a slender clavicle, practically rodlike, imperforate. In *Lepidoblepharis, Pseudogonatodes* and *Coleodactylus* the clavicle is slightly dilated, but also imperforate. In *Sphaerodactylus* it is little broader than in *Coleodactylus,* but with a distinct fenestra. The interclavicle is cruciform in all genera, but in *Gonatodes* the transverse arms are obsolete, approaching a dagger-like shape.

4. *Superciliary scales.* All genera but *Gonatodes* have the skin of the superciliary region produced into a fold, the anterior granules of which are usually enlarged into flat scales. In *Sphaerodactylus* there is a conspicuous horny spine on the fold; a similar spine is found in *Gonatodes hasemani.* In *G. caudiscutatus* there are up to 3-4 spines, varying in size and number, within a sample and on both sides of the same specimen; at least part of this variaton seems due to wear.

5. *Sexual dimorphism in ventral pholidosis.* Grant (1931) first noticed the presence of an area of enlarged scales ("escutcheon") on the lower belly and thighs of male *Sphaerodactylus.* Noble & Klingel (1932) thought this area similar to preanal pores. Taylor & Leonard (1956) extended the findings to *Gonatodes* and *Lepidoblepharis,* and made a histological study, concluding that "the relationship of these scales to the preanal and femoral pores is uncertain". Taylor & Leonard did not find an escutcheon in *Pseudogonatodes.* I confirm their results and report the absence of the structure in *Coleodactylus.*

6. *Sexual dichromatism.* All species of *Gonatodes* show strong sexual dichromatism. Adult males are boldly patterned and brilliantly colored, often with a sharp contrast between head and trunk. These colours disappear with preservation. Females and young males are more soberly colored and do not change with preservation. In *Sphaerodactylus* some species are known to be dimorphic, others not. I have seen alive both sexes of *Coleodactylus amazonicus* and *meridionalis* and noticed no dichromatism. For *Pseudogonatodes* and *Lepidoblepharis* there is no information on live specimens.

Underwood (1954) believes that dichromatism is related to diurnal life. This is certainly probable, but is not the whole story, as *Gonatodes humeralis* and *Coleodactylus amazonicus* live in the same forest, are both diurnal, and only the former is dichromatic. Very probably, as suggested by E. E. Williams, the reason of the difference is that *Gonatodes* is arboreal and *Coleodactylus* lives in leaf litter.

7. *Inner ear.* Hamilton (1960, see discussion in Vanzolini, 1968) studied *Gonatodes, Lepidoblepharis* and *Sphaerodactylus.* It is quite evident that the first named is closest to the Gekkoninae. As to the other two, Hamilton (p. 1011) says: "... there seems to be a trend in the development of sensory areas of the saccule and cochlear duct in the Sphaerodactylidae that indicates that *Lepidoblepharis* is more advanced than *Sphaerodactylus*".

8. *Size.* The Sphaerodactylinae are small geckos. *Gonatodes* is consistently the largest-bodied genus; however, it seldom reaches more than 50 mm rostro-anal length, which is below the average for South American Gekkoninae. The species of the other genera are usually diminutive, one *Lepidoblepharis* being possibly the smallest Recent lizard (Dunn, 1944); however, *Pseudogonatodes furvus* and *Sphaerodactylus copei* are as large as many *Gonatodes.*

*Conclusion.* The sequence of morphological stages of the ungual sheath first analysed by Parker (1926) is so seductive that one tends to interpret sphaerodactyline evolution as a linear series, *Gonatodes — Lepidoblepharis — Pseudogonatodes — Coleodactylus — Sphaerodactylus.* In fact, many characters fall into this sequence, but others do not

The basal position of *Gonatodes* seems real and is enchanced by several other important characters: amphicoely, simplicity of the periocular lepidosis, structure of the inner ear and size. Kluge (1967) lists other primitive skeletal characters: presence of a large, unreduced coronoid, of a large squamosal and of a large, unreduced paroccipital process of the opisthotic.

Underwood (1954), never having seen *Coleodactylus,* supposing *Gonatodes* procoelous and writing before the otological studies of Baird (1960) and Hamilton (1960), accepted the sequence in general, but in the inverse direction (p. 487): "A clear implication of the proposed classification is that the procoelous condition is primitive in geckos and the amphicoelous condition secondary", and "... more probably however the members of the genus *Gonatodes* are secondarily padless."

Kluge (1967) prefers to think that primitive geckos were procoelous, but primitive sphaerodactylines amphicoelous, and I accept this viewpoint.

As to the matter of the *Gonatodes* digital structure being primitive or secondary, Underwood (1954:483) thinks the loss of the pad to be "no doubt associated with reversion from scansorial to terrestrial habits". However, *Gonatodes humeralis* lives on tree trunks and is padless; *Coleodactylus amazonicus* lives in the leaf litter of the same forest and has a globose sheath, which Underwood equates with a pad. Kluge (1967) also believes the digital structure of *Gonatodes* to be primitve.

With regard to the morphology of the shoulder girdle, one could construct a linear series from rod-like imperforate clavicles (*Gonatodes*) to slightly dilated, imperforate (*Lepidoblepharis, Pseudogonatodes, Coleodactylus*) to dilated, fenestrate ones (*Sphaerodactylus*). If we take the general gekkonid condition (clavicle medially dilated and fenestrate) as primitive, the sequence would read from *Sphaerodactylus* to *Gonatodes*. But the opposite direction can be defended: "It is perhaps reasonable to assume that the clavicle in the primitive Squamata was of the simple rod type..." (Romer, 1956: 302).

The situation of the inter-clavicle would be parallel: it is cruciform in all genera but *Gonatodes,* in which it is dagger-like, as in the majority of Gekkoninae.

Other characters cannot be arranged in linear sequences agreeing with that discussed above. The escutcheon is absent in *Pseudogonatodes* and *Coleodactylus.* Sexual dichromatism is known only in *Gonatodes* and *Sphaerodactylus.* The structure of the sensory surfaces of the inner ear is more advanced in *Lepidoblepharis* than in *Sphaerodactylus.*

I believe it is plausible to say that the Sphaerodactylinae are a small and possibly old group, which branched off from the general gekkonid stock at a stage no longer represented by any living species; it presents its own evolutionary trends and sequence, which can be imagined to be as follows:

1. Basal stock diurnal, with simple digits, free claw, amphicoelous vertebrae with thick intervertebral disks, rod-like clavicles, interclavicle dagger-shaped, periocular region with an incipient fold.
2. Loss of voice and eventual correlated otic modifications.
3. Elaboration of an ungual sheath and, secondarily, asymmetrical dilation with acquisition of the added functions of a pad.
4. Development of procoelous vertebrae (contrary to general gekkonid trends).
5. Medial dilation and fenestration of the clavicle; loss of the cross arms of the interclavicle (parallel to general gekkonid trends).
6. Development of pseudo-palpebral (superciliary) folds, with spines.
7. Sexual dichromatism.
8. Development of a ventral escutcheon in males.
9. Dwarfism.

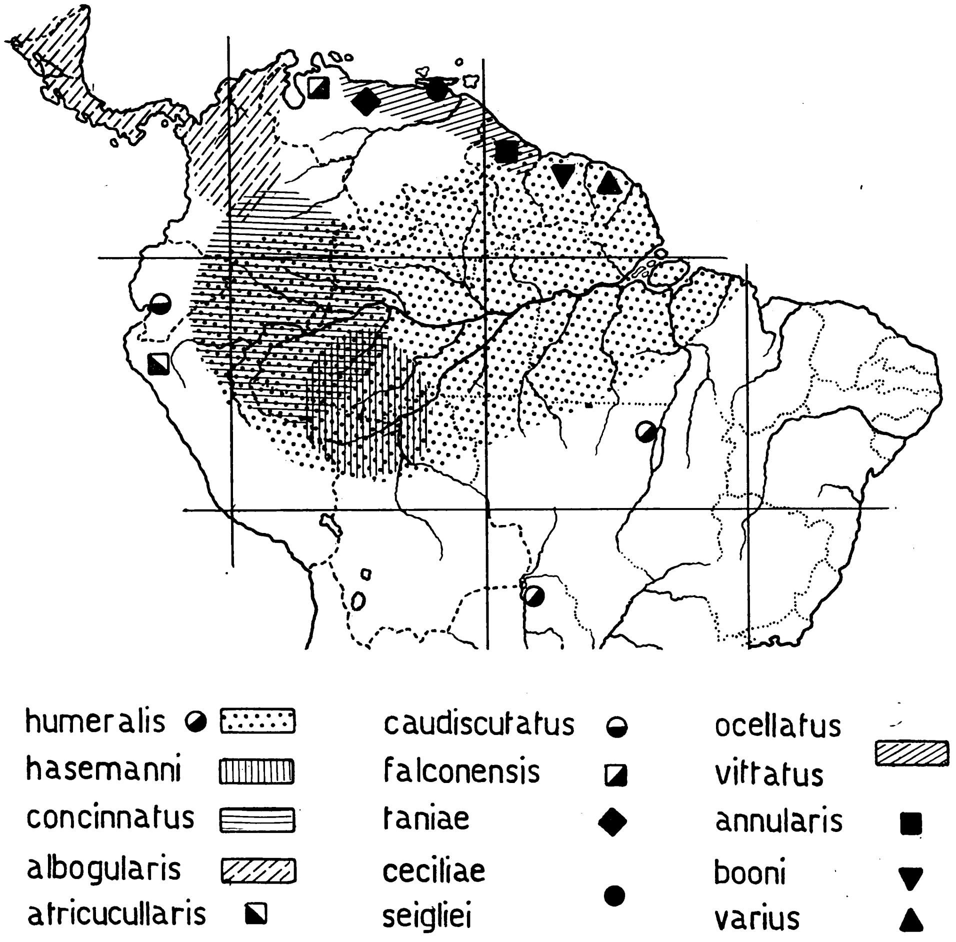
These tendencies, or evolutionary potentials, are differently expressed in the existing genera (a mild case of mosaic evolution). Thus *Gonatodes* would be closest to the stem in all characters except the presence of dichromatism and of an escutcheon. *Lepidoblepharis* and *Pseudogonatodes* would be early offshoots of the main stem. *Coleodactylus* would be primitive in the absence of dichromatism and of an escutcheon, but advanced in shoulder girdle morphology and, especially, digital structure. *Sphaerodactylus* would be the most differentiated genus in all characters but otic structure.

## DISTRIBUTION OF THE SPHAERODACTYLINAE

### GONATODES (Map 1)

The distribution of *Gonatodes* can be studied only on the basis of records that are very well documented or have been personally checked. The literature is ridden with misidentifications, especially of females (see Vanzolini, 1968, synonymic lists). Furthermore, the present data will certainly be much modified with further collection and with revision of the available materials.

However, a clear pattern emerges from the map. There is one species with broad Guiano-Amazonian distribution, *G. humeralis*. There are two records from Urucum, southwestern Mato Grosso (Peracca, 1904; Parker, 1928), far from the hylaea, and one from Barra do Tapirapés, northern Mato Grosso (Vanzolini, 1968), near the hylaea but in the cerrado. Another form, *albogularis*, extends from Colombia into Central America and the West Indies (Vanzolini & Williams, 1962). The remaining forms have much smaller ranges, all peripheral to Amazonia. Two forms which belong in the valley (*hasemani* and *concinnatus*) do so in restricted areas near the western edge. Several of these allopatric forms may turn out to be subspecies, but this is not relevant to the present argument.



Map 1. Approximate distribution of *Gonatodes* on the mainland.

This pattern of *Gonatodes* can be interpreted in two ways. One would be according to Brown's (1957) "central-peripheral" model. The other would involve differentiation along the northwestern belt from the Guianas to Ecuador, with secondary invasion of Amazonia.

Brown's model would imply successive pulsations of the range of an Amazonian basal stock. Retreats would leave isolated peripheral populations, as some kind of "witnesses" of the evolutionary path of the group. This means that *humeralis,* inhabiting the core of the territory, would be the most advanced species.

The idea of strongly pulsating ranges in South America — in much more recent times, in a much more drastic fashion and much more frequently than usually believed — is one that is gaining strength from geomorphic (Vanzolini & Ab'Saber, 1968) and palynological (Gonzales & al., 1966) data. But I believe Brown's model does not apply in this case. A very strong point against it is the relative lack of agressiveness of the genus towards the south and, especially, its absence in the Atlantic forest. The only signs of spread southwards are the records of *G. humeralis* from the two localities in Mato Grosso, outside the hylaea. I have seen no specimens from southwestern Mato Grosso but have no reason to challenge the identifications, especially Parker's, as he knew the species perfectly well (Parker, 1953a).

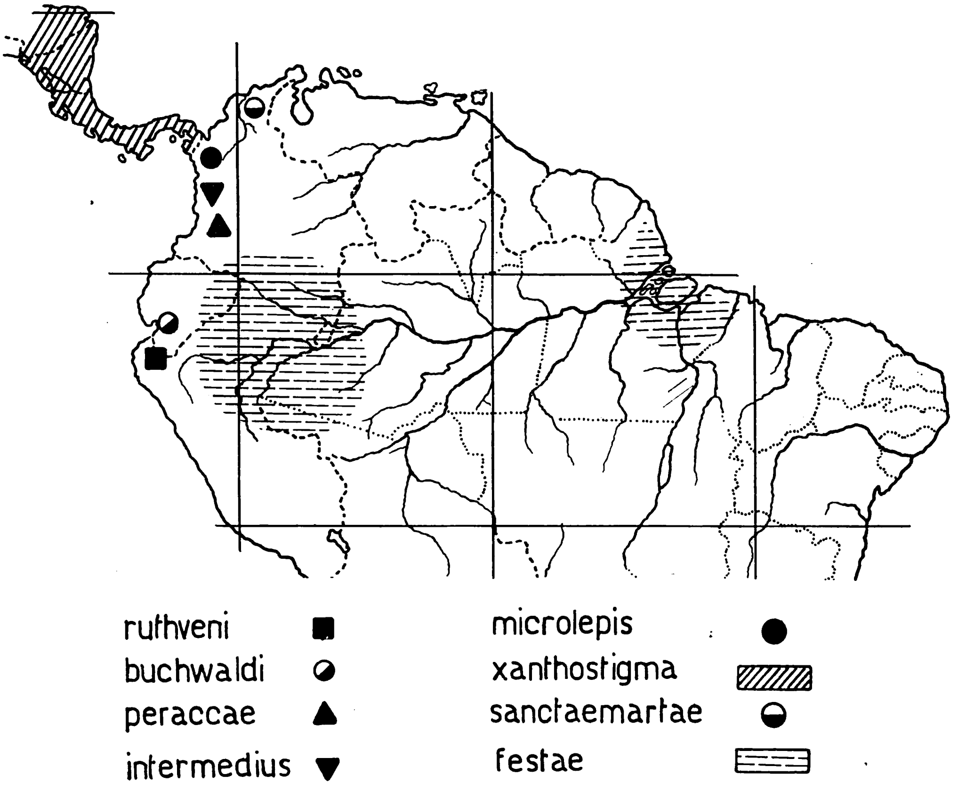
The absence of *Gonatodes* in the Atlantic forest is a serious matter. Numerous Amazonian forms (*Lachesis muta, Corallus cooki, Anolis punctatus, Anolis ortoni, Dendrophidion dendrophis, Tripanurgos compressus*) occur in its warmer (northern) part, in spite of the broad belt of open formations which presently separates the two forested areas (Vanzolini, 1963). It is hard to believe that successive pulsations of Amazonian populations would have left no traces in the Atlantic forest.

I am thus inclined to believe that *Gonatodes* developed outside Amazonia, and invaded it at some later time.

This leads to the consideration of an area of great zoogeographic importance, that I propose be called the "northwest arc" (in Portuguese "arco de noroeste"). This is the transmontane, circum-Amazonian belt extending from the Guianas to Ecuador. The central, Colombian, part of this belt has been called by Simpson (e.g. 1950), a "filter zone", as it marks the extreme southern limit of many Nearctic vertebrates. I believe the area should be extended from the Guianas to Ecuador, to include the distribution of many northern (not obligatorily Nearctic, though, some are Meso American) elements, such as *Chelydra* (Colombia to Ecuador), *Sphaerodactylus* (Guiana to Ecuador), *Cryptotis* (Venezuela to Ecuador), etc. On the other hand, the term "filter" is not very adequate because not all forms presently limited to the arc are northern immigrants there detained. Two groups at least (*Tremarctos,* the spectacled bear, and the caenolestid marsupials) are now restricted to the arc, but have been in the past (respectively in the Pleistocene and during all of the Tertiary) widely distributed in Brasil. Turtles of the genus *Pseudemys* would present the same pattern, and very convincingly, but for one disjunct species in southernmost Brasil, Uruguay and adjacent Argentina (Williams, 1958).

This arc is certainly a buffer belt between Central America and the Guiano-Brasilian region. But, as shown by *Gonatodes* and (below) by *Pseudogonatodes* and *Lepidoblepharis,* it most probably has functioned also as a center of evolution for several groups. It is a much dissected region, with diversified climate and vegetation; one can hardly imagine a better stage for geographical differentiation (Chapman, 1917), especially keeping in mind the Quaternary climatic vicissitudes of the region (for references, see van der Hammen, 1956; Gonzales, van der Hammen & Flint, 1966).

I consider it probable that the cycles of speciation of *Gonatodes* which determined its present pattern of distribution happened mainly in this northwest arc, and that invasion of Brasil has been secondary. *G. concinnatus* and *G. hasemani* must have arisen in consequence of modern ecological changes in Amazonia, possibly the same which determined the pattern of speciation of the *Anolis* of the *punctatus* group (Williams & Vanzolini, 1966), also in western Amazonia.



Map 2. Approximate distribution of *Lepidoblepharis.*

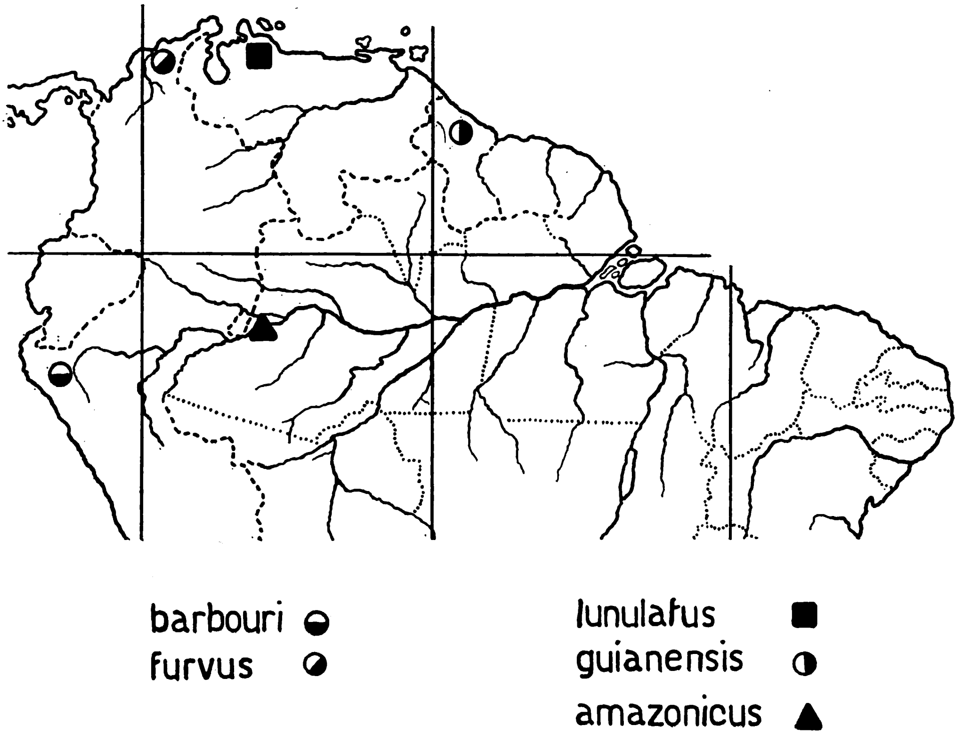
### LEPIDOBLEPHARIS (MAP 2)

The distribution of *Lepidoblepharis* resembles that of *Gonatodes*. There are 6 species with small ranges in the western half of the northwest arc (from the Sierra Nevada de Santa Marta to southern coastal Ecuador), one species (*festae*) with an enormously broad Amazonian range, and one Centro-American species (*xanthostigma*).

I have compared eastern and western specimens of *festae* and found no differences. It is very probable that the history of *Lepidoblepharis* is too recent to have permitted differentiation.

### PSEUDOGONATODES (MAP 3)

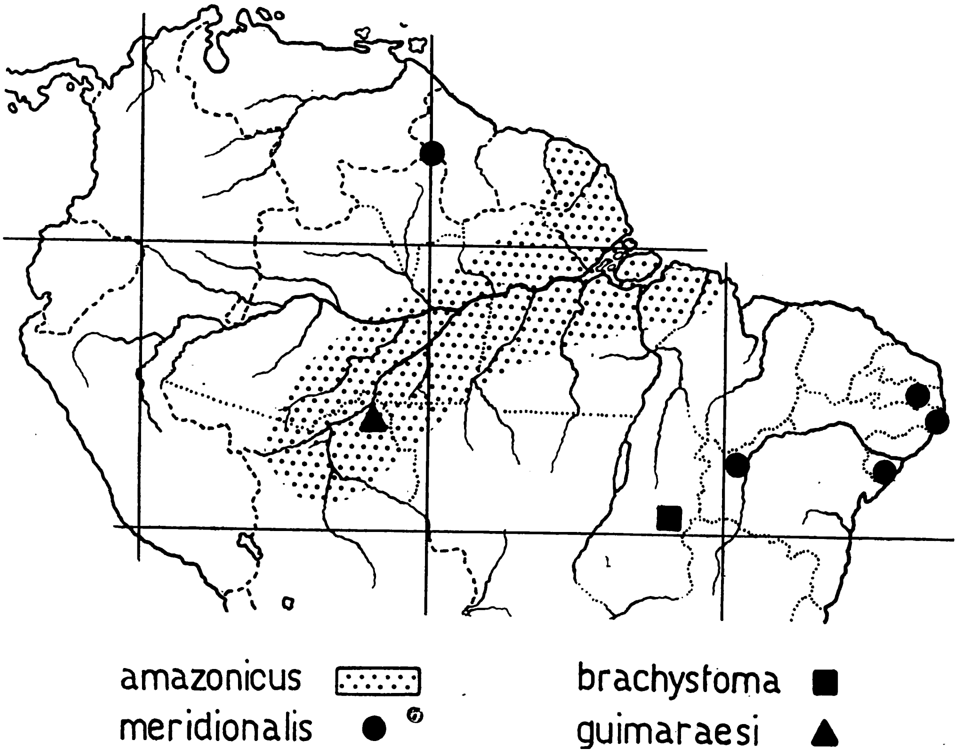
The distribution of *Pseudogonatodes* is fundamentally similar to that of *Gonatodes* and *Lepidoblepharis*: it has 4 species in the northwest arc and one in western Amazonia; none is known to be widespread. With exception of the outlying *barbouri*, the forms of *Pseudogonatodes* are so homogenous (Vanzolini, 1967) that it is possible that they are races of a single kreis. It is curious to note that, although the Amazonian form is on the upper Solimões, its closest relative seems to be the Guianan form.



Map 3. Approximate distribution of *Pseudogonatodes*.

### COLEODACTYLUS (MAP 4)

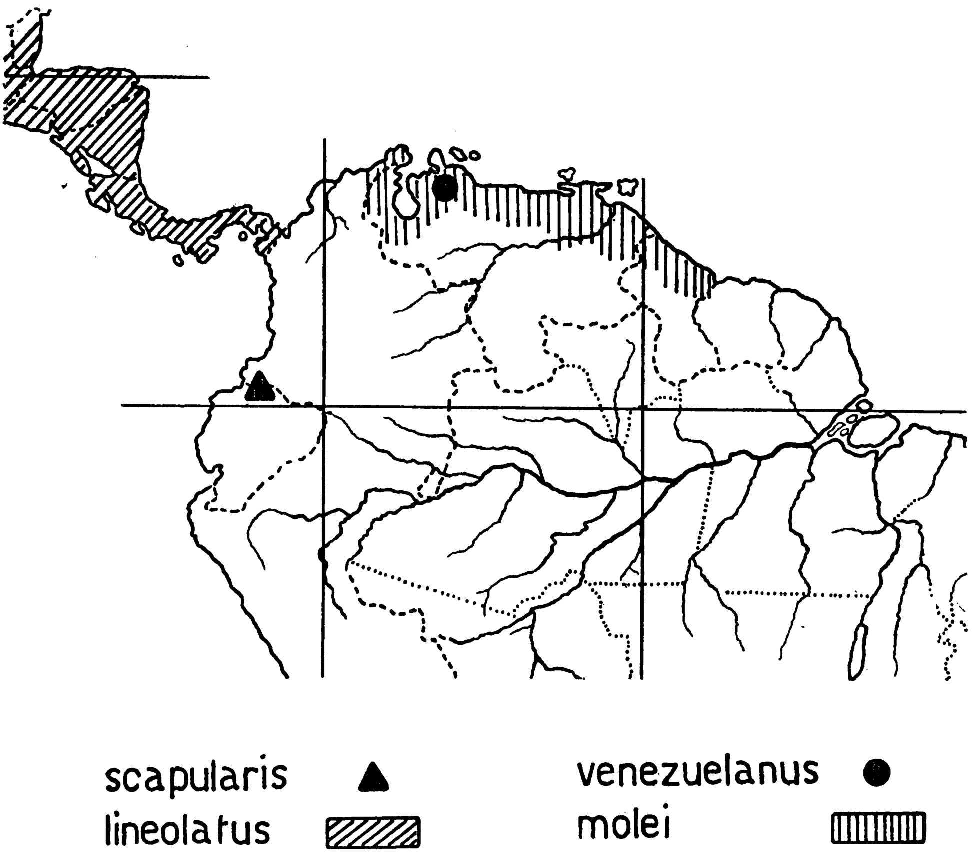
The distribution of *Coleodactylus* radically differs from that of the preceding genera. Its center of gravity is undobtedly Amazonian, and one is led to consider a rather different history. There are two species, *meridionalis* and *brachystoma*, that are presumably more primitive (smooth dorsal scales, less assymmetrical digits) and two that are more advanced (*amazonicus* and *guimaraesi*). In fact, the relationship between the latter two is not very clear, it being possible that they are subspecies or even synonyms.



Map 4. Approximate distribution of *Coleodactylus*.

The species of *Coleodactylus* are leaf-litter dwellers inside the forest. *C. brachystoma* is known from a restricted area in eastern Goiás. *C. meridionalis* has a most interesting disjunct distribution. It is known from several isolated patches of forest in northeastern Brasil, some of which are relicts of the northern end of the Atlantic forest, but one at least being too far inland for that. There are no means of present contact between populations, as they are separated by broad xerophytic areas. Furthermore, there are two records from the Brasil - [British] Guyana border, separated from the rest of the range by the whole width of the hylaea, in which the species has not been found. These two suprising northern records have been reported by Parker (1935) and by myself (Vanzolini, 1957), both of whom had at hand northeastern specimens for comparison. *C. amazonicus* is broadly distributed in Amazonia and the eastern Guianas. *C. guimaraesi* is known from one specimen in southwestern Amazonia.

To explain this distribution one has to accept at least two cycles of speciation. During the first one *brachystoma* and *meridionalis* evolved. The range of the latter must have been continuously forested, either at this time or during a successive phase of spread. The present disjunction in the south is certainly consequent to deterioration of the plant cover during the semi-arid phase through which the region is now passing. The Amazonian disjunction is easily explained by postulating that *meridionalis,* formerly widespread at least in eastern Amazonia, has been pushed out of the hylaea by competing, and more successful, *amazonicus,* and is now restricted to marginal habitats. The lack of differentiation of *meridionalis* may be due to evolutionary conservatism, or to recency of the distributional phenomena discussed, or,



Map 5. Approximate distribution of the species of *Sphaerodactylus* that occur in continental South America.

more probably, to a combination of both factors. *C. guimaraesi* (if a good species) is located in the same general area where *Gonatodes* has differentiated within the hylaea.

### SPHAERODACTYLUS (MAP 5)

This genus is extremely abundant throughout the Greater and Lesser Antilles, where numerous endemic forms occur. In Central America and Mexico there are about 6 species, the northern limit of the distribution being Vera Cruz and Oaxaca. In continental South America there are 3 species, all in the northwest arc: *molei* (Guiana and Venezuela, plus Trinidad); *venezuelanus* (Falcón, coastal Venezuela); *scapularis* (western Colombia and Ecuador, Gorgona Island). A central American species, *lineolatus,* probably enters Colombia adjacent to Panamá.

Ist seems clear that this is a Meso American element, which has been able to colonize the Caribbean and to get a foothold in the northwest arc, but not in the core of South America.

### SUMMARY

We have thus three geographical elements among the sphareodactylines: (i) one Meso American (*Sphaerodactylus*); (ii) one northwestern (*Gonatodes, Lepidoblepharis, Pseudogonatodes*); (iii) one Amazonian (*Coleodactylus*). The origin of the group as a whole would lie in the northwest arc. *Coleodactylus* seems to be the product of an invasion of Amazonia, earlier than but similar to that of *Gonatodes* and, to a lesser scale, *Lepidoblepharis* and *Pseudogonatodes*. *Sphaerodactylus* would be the result of the radiation of an immigrant into Central America.

## THE GENERA OF GEKKONINAE

I accept provisionally ten gekkonine genera in South America: *Homonota, Garthia, Gymnodactylus, Phyllopezus, Bogertia, Briba, Hemidactylus, Thecadactylus, Phyllodactylus* and *Lygodactylus.* The general systematics of the subfamily is unsatisfactory, as can be seem from Wermuth's (1965) recent check list and from the pertinent notes in Vanzolini (1968). There are many unwieldy, poorly defined genera, side by side with scarcely justifiable monotypic ones. Kluge (1967), redefining the subfamilies Gekkoninae and Diplodactylinae, has improved the understanding of the general pattern of distribution, but for a consideration of generic patterns it is clear that a series of revisions is in order.

Meanwhile, I think digital structure continues to be the best first approach to the study of a local fauna, especially a small one such as the South American. There are several patterns sufficiently differentiated to ensure that a given lineage will adhere to its "chosen" adaptive course, shifts between major types being improbable. I have doubts only with regard to the forms with simple digits, which may convergent.

The following patterns of digital structure are found in South American gekkonines:

1. Digits not dilated: *Homonota, Garthia, Gymnodactylus.*
2. Digits entirely dilated, fringed: *Thecadactylus.*
3. Digits dilated only distally: *Phyllodactylus.*
4. Digits dilated only proximally, the distal phalanx compressed and arising from
    - 4.1. the middle of the expanded portion: *Hemidactylus, Phyllopezus, Briba, Bogertia.*
    - 4.2. the distal end of the expanded portion: *Lygodactylus.*

## THE GENERA WITH SIMPLE DIGITS

The taxonomy of this group has been fraught with vicissitudes (details in Vanzolini, 1968) and is far from settled. I presently accept the following scheme:

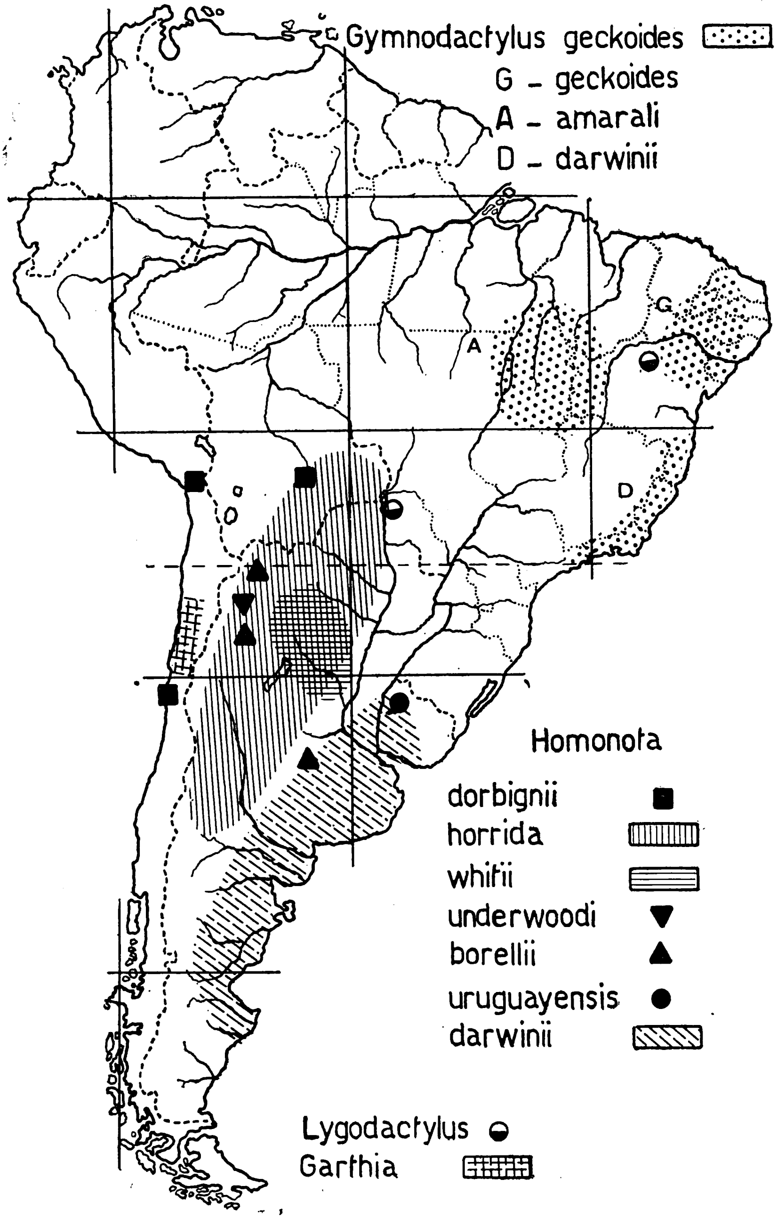
1. *Homonota* (digits straight, simple, pupil lobate, ceratobranchials II present): *borellii, darwinii, dorbignii, horrida, mattogrossensis* (doubtful), *pasteuri* (doubtful), *underwoodi, uruguayeensis, whitii.* I exclude *pasteuri* (name proposed by Wermuth, 1965, for *fasciata*) from present consideration; it is known only from the type, an old specimen from a very suspect early 18th century locality, "Martinique", far from the range of the well-documented species. *H. mattogrossensis,* judging from the description, is probably a synonym of *horrida* as maintained by Kluge (1964); however I think it wiser to take a final decision on the basis of Mato Grosso specimens with precise localities; they have been so far unavailable.

2. *Gymnodactylus* (distal phalanges forming an angle with the basals, digits simple, pupil straight, ceratobranchials II absent): *geckoides,* with 3 subspecies, *geckoides, amarali* and *darwinii.* Kluge (1967), contrary to Wermuth (1965) maintains *Cyrtodactylus* (Old World) and *Gymnodactylus* (South American) as separate genera, as originally proposed by Underwood (1954). As Wermuth's subgenus *Gymnodactylus* corresponds exactly to the full genus of the other authors, the matter is not too relevant in the present context.

3. *Garthia* (digits straight, with ungual sheath, pupil lobate, ceratobranchials II present): *gaudichaudii.* It may be argued that, since *Garthia* is an obvious offshoot of *Homonota,* from which it differs in only one character, there would be no point in erecting a monotypic genus. I believe, however, that the acquisition of an importante digital adaptation, marking a new evolutionary path, should be emphasized by taxonomic rank. Klüge (1964, 1967) does not mention this ungual sheath.

The relationships between *Homonota* (plus *Garthia*) and *Gymnodactylus* (as represented by *geckoides*) are not clear. I find a great difference in hyoid morphology; the cornu of *Homonota* and *Garthia* has a pair of backward-directed projections (probably ceratobranchials

II), which are lacking in *G. geckoides*, whose hyoid is of the typical gekkonine type. I am inclined to believe that the two groups represent two separates stocks, but no definite statement is possible before a good general treatment of the subfamily.



Map 6. Approximate distribution of *Gymnodactylus*, *Homonota*, *Garthia* and *Lygodactylus*. *Homonota* after Kluge, 1964, and Gallardo, 1966.

DISTRIBUTION (MAP 6)

With the exception already mentioned of *H. pasteuri*, *Homonota* is an Andino-Patagonian genus, extending from southern Bolivia, Paraguay, northern Argentina and Uruguay into Chile (*H. dorbignii*, to Valpariso) and Patagonia (*H. darwinii* to Puerto Deseado). *Garthia* exists in north-central Chile. I have commented (Vanzolini, 1968) on the small probability of the genus extending as far within Mato Grosso as hypothesized by Kluge (1964).

It seems certain that this is an old southern Andino-Patagonian element. The area of maximum sympatry is in northwestern Argentina and adjacent Bolivia (*whitii, horrida, borelii, underwoodi*). I am unable to interpret this pattern of distribution in terms of the faunal history of South America, but must note that a closely similar picture is found in *Leiosaurus* (Gallardo, 1961).

The only species of *Gymnodactylus* s.s., *G. geckoides*, has a most interesting distribution (Vanzolini, 1953a). It extends from Rio Grande do Norte, in northeastern Brasil (ca. 6°S) to S. Paulo (ca. 23°S), inland as far as eastern Mato Grosso. Its three races seem to be associated with three major Brasilian plant formations: *g. geckoides* with the xerophytic caatingas, *g. amarali* with the savanna-like cerrados and *g. darwinii* with the Atlantic forest. This does not seem a very old distributional pattern, especially since the differences between *geckoides* and *amarali* (the two open formation races) are not too sharp. *G. g. darwinii*, the forest form, is well set-off.

The ranges of *Homonota* and *Gymnodactylus* as known at present are widely separate; the intervening region, however, still keeps some surprises: for instance, *Lygodactylus* has been very recently discovered there. Anyway, even if some degree of overlap comes to be found, it is safe to ascribe to the two groups entirely separate areas of differentiation. *Gymnodactylus*, which does not occur in Amazonia and is only in the middle third of the Atlantic forest, must have differentiated in the norteastern half of the diagonal belt of open formations which extends from northeastern Brasil to the Chaco (Vanzolini, 1963); *Homonota* differentiated either in the southwestern end of this same belt or in northern Argentina. On the Paficic coast it should be noted that *Phyllodactylus* and *Homonota* overlap very slightly.

## HEMIDACTYLUS AND RELATED GENERA

There is in the world an abundance of geckos with lobate pupil and with the proximal phalanges dilated into a pad, from the middle of which emerges the compressed distal phalanx. As a result of the large number of species, with practically worldwide distribution, their systematics on the generic level is very unsatisfactory. Genera are defined on the basis of trivial characters, such as the degree of development of the first digit and its claw, the entire or divided character of the scansors and the type of dorsal lepidosis. Furthermore, not even these criteria are always consistently applied. Nothing definitive can be done in this group without a global study, but it is possible to examine the situation of the South American forms.

Currently recognized are one species of the widespread genus *Hemidactylus* (until recently considered as an endemic form, *leightoni*, but now said by Kluge, 1967, to belong to the widespread species *brooki*), and three monotypic endemic genera, *Phyllopezus*, *Bogertia* and *Briba*. *H. mabouia*, introduced by man, is not considered here. The relevant characters are summarized in Table 1.

TABLE 1

SOUTH AMERICAN HEMIDACTYLOID GENERA

| | *H. brooki* | *Phyllopezus* | *Bogertia* | *Briba* |
|---|---|---|---|---|
| Lamellae | Double | Single | Single or incised | Double |
| Pollex | Strong | Strong | Rudimentary or absent | Reduced |
| Hallux | Strong | Strong | Strong | Reduced |
| Dorsal tubercles | Present | Present | Absent | Present |
| Caudal tubercles | Present | Absent | Absent | Present |

It is immediately apparent that *Briba* is characterized only by the reduction of the pollex and hallux. The combination of characters used to define *Phyllopezus* (lamellae single and non tuberculate tail) is found in *Hemidactylus fasciatus* of West Africa. *Bogertia* would be the most diferentiated genus, but, (i) purely granular dorsals are found in several species of *Hemidactylus*, (ii) the lamellae of *Bogertia* are clearly transitional between single and double, and (iii) its pollex is variable in size.

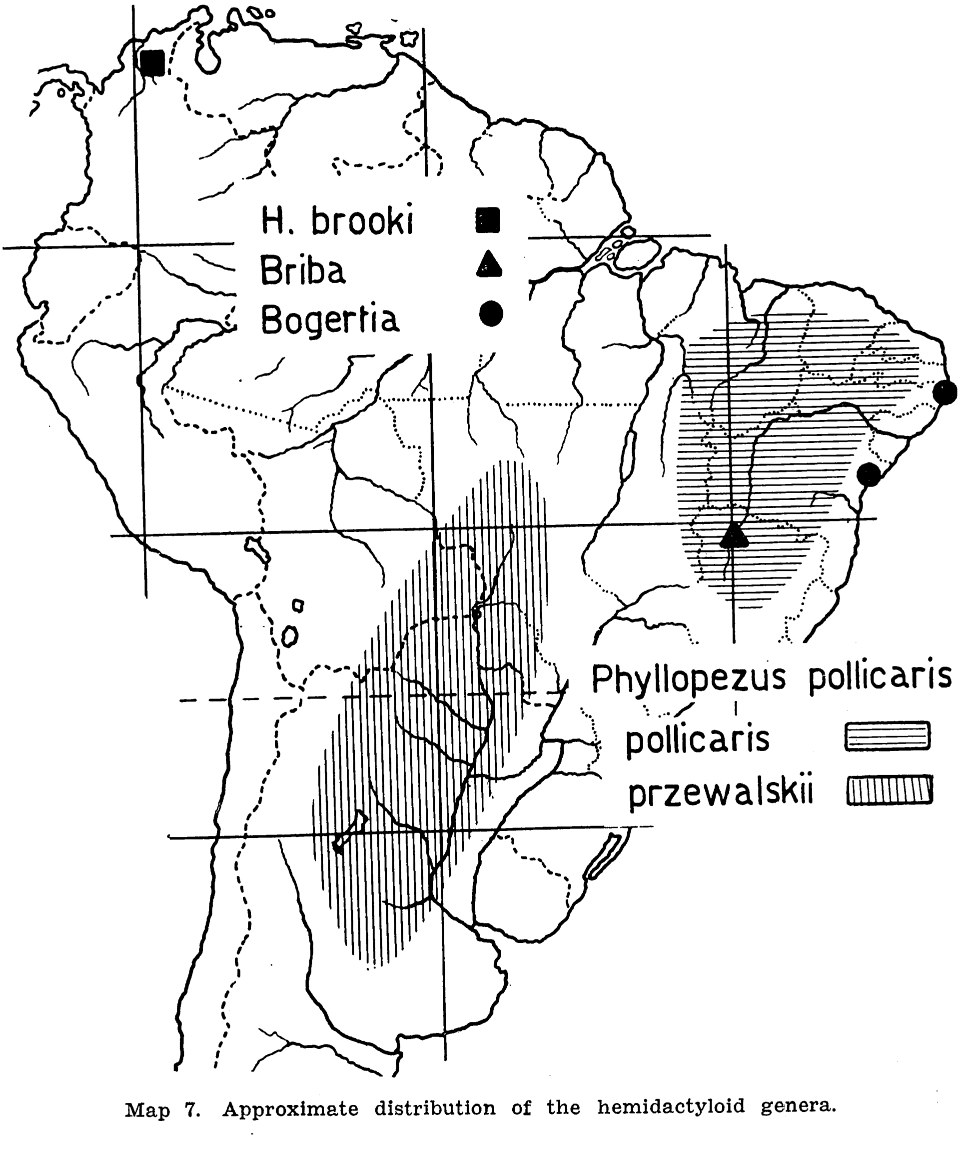
These facts would justify the inclusion of *Bogertia* and *Phyllopezus* into *Hemidactylus* and of *Briba* into *Gehyra* or *Hemidactylus*. On the other hand, these genera, as presently conceived, are highly heterogeneous, and assigning the Brasilian species to them would add nothing to the understanding of the situation. I prefer for the time being to leave the names as they are, but to treat the distribution of the four genera as a unit.

### DISTRIBUTION (MAP 7)

*Hemidactylus brooki*, present in many Caribbean localities, occurs in a small area of northern Colombia. The other species are cis-Amazonian.

*Bogertia lutzae* is known from two coastal localities, one in Bahia and the other in Pernambuco; it inhabits (during the day) ground bromeliads growing on sand dunes. *Briba brasiliana* is known from two localities in northern Minas Gerais, Jatobá, in the Serra do Espinhaço, and Rio dos Pandeiros; nothing is known of its ecology.

*Phyllopezus pollicaris*, with two subspecies (Vanzolini, 1953a; Hellmich, 1960) is extensively distributed along the diagonal belt of open formations mentioned above and enters deeply into Argentina (Gallardo, 1966). I have collected the nominal race in the driest



Map 7. Approximate distribution of the hemidactyloid genera.

caatingas of northern Bahia and in the cerrados of Maranhão and Goiás. It apparently intergrades with the southwestern race, *pollicaris przewalskii,* in western Goiás. Thus, the present distribution is not determined by the type of plant formation. It is more plausible to believe that the two stocks were isolated into areas of open formations separated by the connection between the Amazonian and Atlantic forests cited in the case of *Coleodactylus.*

In summary, three out of four species in this group are narrowly distributed and widely allopatric. The fourth species (*P. pollicaris*) has a large territory, and is apparently undergoing a cycle of expansion and differentiation. The whole group is strictly non-Amazonian.

## THECADACTYLUS

This is the largest-bodied South American gecko. It is a nocturnal forest dweller. Its digital structure is unlike anything else in the continent: the digits are very broad in all their length, distinctly fringed, partly webbed. The lamellae are divided by a deep longitudinal sulcus into which the claw is retractile.

The southern limit of the distribution is the edge of the hylaea, the northern one Yucatan. There is no critical evidence by which to judge its area of origin.

## PHYLLODACTYLUS

Dixon, who has done most of the recent work on New World *Phyllodactylus,* and on whose papers I have based my data, except for the forms of the Pacific coast of South American, says (1964: 16) that "The range of the genus is essentially that of the deserts and semi-arid tropics of the Neotropical Realm". However, inspection of Dixon's Map 1 (which he permits me to copy as Map 8) shows that, although *Phyllodactylus* is restricted to such environments, it does not occupy all the xeric intertropical areas of South America: for instance, no form occurs in the xerophytic areas of Brasil.

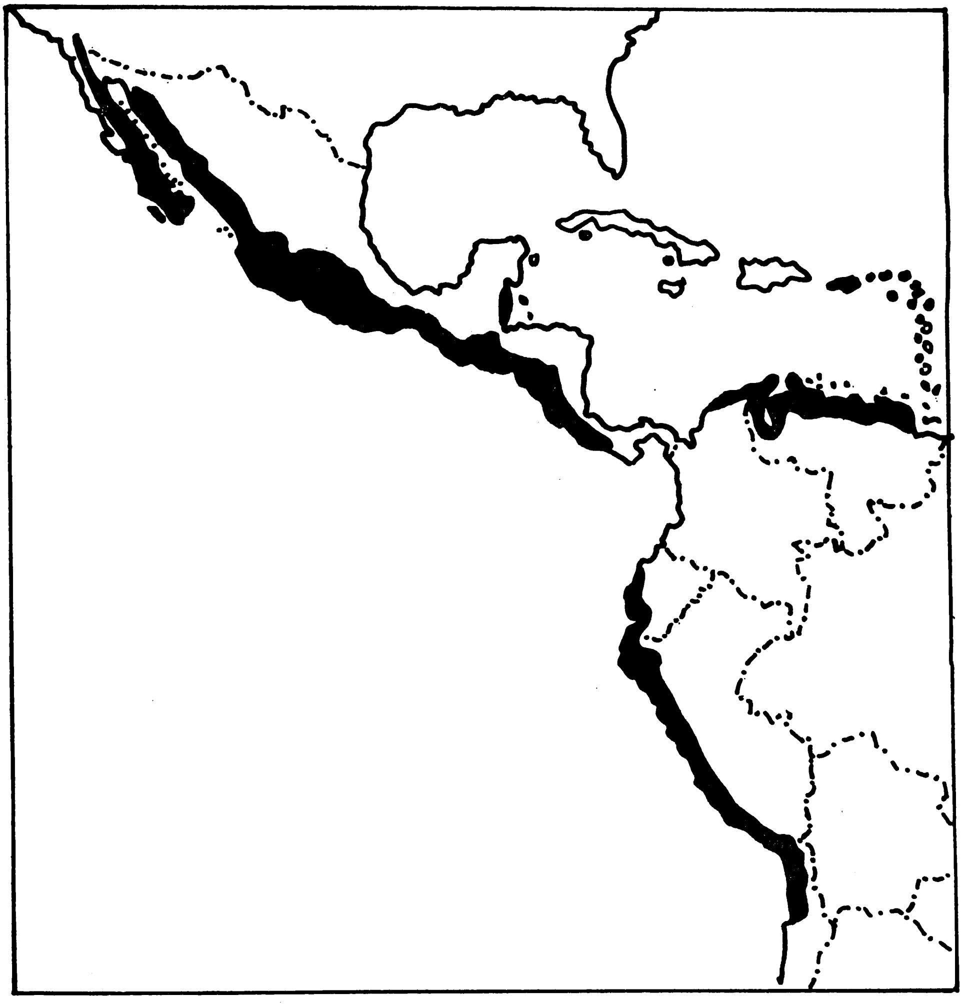
From the map one can see that there are three major areas of occurrence of *Phyllodactylus* in the Americas:

1. *The Pacific coast of North and Central America.* Dixon (1964a) records 12 species from Baja California to Costa Rica.

2. *Western South America.* From Ecuador to northern Chile 13 species are listed. Of these, 3 are recorded from the eastern side of the Peruvian Andes (Vanzolini, 1968): *baessleri* (Chanchamayo, in Junin), *magister* (valleys of the upper Marañon) and *phacophorus* (from the coast, in Lima and Piura, to Cajamarca and Junin). Six species occur in the Galapagos islands (van Denburgh, 1912).

3. *The Caribbean.* One race (*ingeri*) of a species (*tuberculosus*) from the Pacific slope occurs on the coast of British Honduras. Another species (*insularis*) of the same species group is found in Half Moon Cay (British Honduras) and, possibly, Roatan Island (Honduras). One species (*wirshingi*) is recorded from Puerto Rico and the adjacent islet

of Caja de Muertos. One species (*ventralis*) ranges from the Santa Marta region in Colombia to northeastern Venezuela, occurring also in two islands (Margarita and Patos). Five species occur in islands from Aruba to Barbados (Dixon, 1964a). *P. wirshingi* belongs to the latter complex.



Map 8. Distribution of *Phyllodactylus* in the Americas, Galapagos Islands omitted (from Dixon, 1964).

A general treatment of *Phyllodactylus* in the world is not available. Dixon (references in Dixon, 1966) has analysed the northern New World forms, but the situation in western South America is confusing. Thus I do not feel encouraged to use systematic data in this study. However, from a consideration of the distributions depicted in Map 8, it seems plausible to say that we have 2 major elements: (i) one on the Pacific coast of Mexico and Central America, spreading into the

Gulf of Honduras and, along the northwest arc, into Colombia, Venezuela, adjacent islands and Puerto Rico; (ii) the other on the coast of South America from Ecuador to Chile, with some penetration inland. Of course these major elements may be composite.

## LYGODACTYLUS

The only South American species of *Lygodactylus* (unnamed at the time of writing, see Vanzolini, 1968) is known from northern Bahia, two localities, and southwestern Mato Grosso, one locality (Map 6). A typical distribution along the diagonal belt of open formations.

## SUMMARY OF DISTRIBUTION INSIDE SOUTH AMERICA

### COMPARTMENTIZATION OF THE CONTINENT

The most impressive fact about the distribution of South American geckos is the presence of three major compartments in the continent (Map 9).

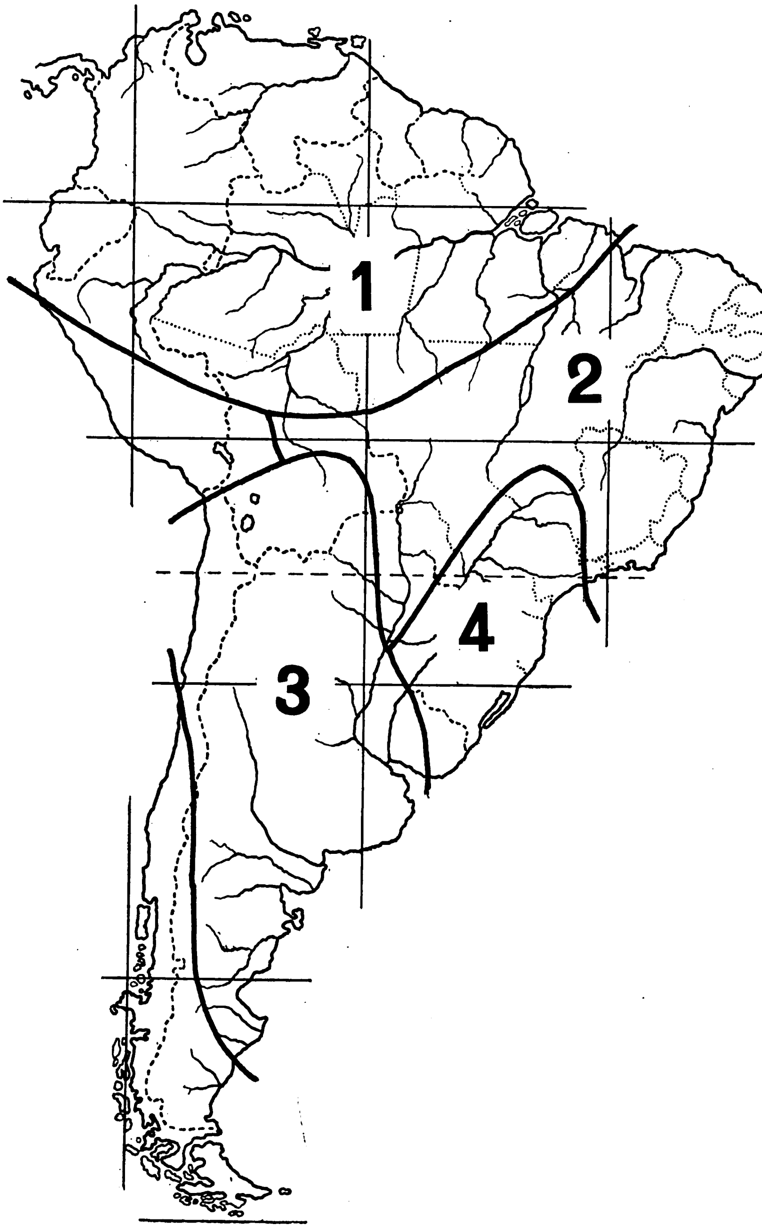
The first compartment extends from the southern edge of the hylaea northwards, continuing into Central America. It is the area of the sphaerodactylines and *Thecadactylus*, and contains two enclaves, *Hemidactylus brooki* and South-Caribbean *Phyllodactylus*. It contains two subunits in South America, the northwest arc and Amazonia, and at least one in Central America.

The second compartment is the area of the hemidactyloids, *Lygodactylus* and *Gymnodactylus*. It contains the enclaves of *Coleodactylus meridionalis* and *brachystoma* and two outposts of *Gonatodes humeralis*, all from the first compartment. Subunits are the diagonal belt of caatingas and cerrados and the northern half of the Atlantic forest.

The third compartment, characterized by *Homonota* and *Garthia*, overlaps the second from southwestern Mato Grosso to Argentina (*Phyllopezus*) and extends into Patagonia and Chile.

This pattern seems to indicate a xeric origin for the whole fauna, with the possible exception of *Thecadactylus*. The forms present in the Amazonian and Atlantic forest appear to be derived from groups primarily situated in the northwest arc and in the belt of open formations. It is remarkable that there exists a large area, in southern Brasil and Misiones (numbered 4 in Map 9) devoid of native geckos. The other empty area of Map 9 (in southern Peru and adjacent Bolivia) is partly inhabited by *Phyllodactylus*, but is also devoid of native geckos inland.

Very little has been done on the ecological biogeography of South America — geomorphic and phytogeographic information is too incomplete and what exists is uneven. It is not possible to undertake a detailed analysis of the broad ecological distribution of the family. There are, however, some indisputable major core areas, which are known to be biogeographical units. I shall discuss five of them: (i) Amazonia; (ii) the belt of cerrados and caatingas; (iii) the Atlantic forest; (iv) the southern Andino-Patagonian region. In addition I shall consider (and begin with) the northwest arc, which I cannot describe as landscape, but which shows distinct faunistic individuality, and the north-central Pacific coast.



Map 9. Compartments of South America based on gekkonid distribution.

*The northwest arc.* This is the area per excellence of the sphaerodactylines, of which no less than 20 forms occur there. In addition, there is one *Hemidactylus*, of world-wide distribution, one *Phyllodactylus*, originating in the Pacific coast, and, in vegetational islands, *Thecadactylus*. The general pattern is one of restricted ranges, well in keeping with the highly diversified landscape.

*Amazonia.* Five genera occur: four sphaerodactylines (*Gonatodes, Lepidoblepharis, Pseudogonatodes* and *Coleodactylus*) and one gekkonine (*Thecadactylus*). The 3 first named genera are immigrants from the northwest arc; the fourth evolved in the valley, but certainly has its primary origin also in the arc. About *Thecadactylus* nothing can be said.

The pattern of differentiation of the sphaerodactylines indicates strong and recent ecological changes in Amazonia, as shown by the speciation of *Gonatodes* and *Coleodactylus* inside the hylaea and by the presence of disjunct populations (differentiated to the species level or not) in vegetational islands in the belt of open formations.

Western Amazonia shows more sympatry and a larger number of forms than the eastern portion of the valley. I attribute this to the vicinity of mountains to the west. These would provide, in dry times, islands of forest, located in suitably oriented valleys, where relict populations could achieve reproductive isolation before the next wet spell and consequent new spread of the forest and its fauna. This mechanism was called upon by Williams & Vanzolini (1966) to explain the distribution of some forms of *Anolis*.

*The belt of open formations.* This extensive area of cerrados and caatingas (see Vanzolini, 1963, and other papers in the same volume) shows enclaves of *Coleodactylus* and *Gonatodes*, and 4 gekkonine genera (and species): *Gymnodactylus, Lygodactylus*, and the hemidactyloids *Phyllopezus* and *Briba.*

*Gymnodactylus* shows differentiation between caatingas and cerrado, and has invaded the Atlantic forest. *Phyllopezus* has two subspecies, on both ends of the diagonal. *Lygodactylus* has a broad distribution, with apparently no differentiation. *Briba* has a very restricted distribution.

To me this whole pattern also indicates ebb and flow of forest and open formations across Central Brasil, with xeric refuges remaining on the geographically and ecologically extreme areas of the Chaco and northeastern Brasil.

*The Atlantic forest.* Two forest geckos occur within the Atlantic forest: *Coleodactylus meridionalis* in the now disjunct vegetational islands of the northermost reaches of the region, and one race of *Gymnodactylus geckoides*, from southern Bahia to the northern coast of S. Paulo, in places penetrating some 160 km inland. Both forms are derived from other core areas, the first from Amazonia and the second from the open formations in Bahia. *Bogertia*, a sand dune gecko, cannot be considered an element of the Atlantic forest. Its case is similar to that of *Liolaemus lutzae* (Vanzolini & Ab'Saber, 1968).

This is a very spotty fauna, and large segments of the Atlantic forest have no native geckos. *Hemidactylus mabouia* is widespread (as well as elsewhere in Brasil) and occupies, besides the perianthropic niche, many "natural" environments.

*The Andino-Patagonian region.* The area from northern Chile and adjacent Bolivia to southern Patagonia is the land of *Homonota* and *Garthia,* with a very complex pattern of speciation. This again seems to be linked to the high mountains of the west of the continent, but I am not competent to comment further on this area. *Phyllopezus* is an element from the cerrado which has deeply entered the region.

*The north-central Pacific coast.* This area, from northern Peru to northernmost Chile, has *Phyllodactylus* as its only gecko. I presume it was once an empty area, similar to that in the Atlantic forest, where Pacific immigrants were able to gain a foothold.

## ORIGIN OF THE FAUNA

I hope it has become clear from the foreging that the fauna of South American Gekkonidae is composed of several disparate groups, with their own patterns of evolution and distribution and thus, possibly, also origin.

The sphaerodactylines are undoubtedly an autochtonous group, with its primary center of differentiation and dispersion in the northwest arc.

Given the world-wide distribution and complex differentiation of the genera with simple digits, it is plausible to say that *Homonota* and *Garthia* are a probable remmant of an old and widespread group, which evolved to its present pattern in the region it still inhabits. *Gymnodactylus* probably represents another offshoot of the same stock, or of a related one, which developed in the Brasilian open formations and invaded the central part of the Atlantic forest.

The relationships of *Thecadactylus* are enigmatical. The only relative suggested, *Pseudothecadactylus,* from the islands in the Strait of Torres, between Australia and New Guinea (Brongersma, 1934), has been placed by Kluge (1967) in a different subfamily.

The genus most relevant to the discussion of the hemidactyloids is *Hemidactylus* itself. It is exceedingly common in the Ethiopian and Oriental regions, and from them it has spread north to the Mediterranean and Japan. It is found in many oceanic islands, having 2 endemic species in Cape Verde and several in the Indian Ocean. Several species have enormous ranges (*frenatus* and *garnotii,* e.g., entering Oceania) but it is difficult in these cases to separate natural dispersal from human agency, which has been certainly many times operative, as in bringing *turcicus* to North America, and *mabouia* to the Neotropical region. *Gehyra,* a related genus, is very successful in Oceania.

*Phyllodactylus* is also extremely widespread, and its distribution resembles that of *Hemidactylus*: Ethiopian and Oriental regions, Mediterranean, Madagascar, Indian Ocean, Australia and Pacific islands as far east as Norfolk Island and the New Hebrides.

*Lygodactylus* belongs to a clear, well differentiated African lineage.

What most forcibly impresses me in this whole picture is the complete absence of relationships with North America. This cannot be easily explained away by recourse to massive extinction of Nearctic annectant forms. The fossil record of the Gekkonidae is not very good (Kluge, 1967), but the weight of negative evidence in the United States cannot be ignored. In spite of the relative lack of Cenozoic beds in the eastern and southern parts of the country, the number of fossil lizards from all areas is large, and among them there is only one gekkonid mandible from the Thomas Farm Miocene of Florida (Estes, 1963). I find particularly important the Lance (Upper Cretaceous) fauna studied by Estes (1964) as, by that time, the recent families were well established (Hoffstetter, 1955) and the two Americas not yet or just recently separated. Estes records 4 teiids, 1 scincid, 2 anguids, 1 xenosaurid, 1 varanid, 2 parasaniwids (extinct family) and 3 genera "incertae sedis", certainly not gekkonid. Some of the forms, especially the teiids, are strikingly modern-looking. Among the still unpublished materials (Estes, *in litt.*) there are no geckos. Even if one keeps in mind (as Estes advises me to do) that the ecology of the Lance may have been unfavourable to geckos (which, are, however, quite versatile nowadays) I think that it is unavoidable to have recurse to heterodox explanations for the origin of the South American geckos with clear and close extra-limital relationships: the hemidactyloids, *Phyllodactylus* and *Lygodactylus*. The others may, for the time being and in the absence of relevant information, be considered as offshoots of Cretaceous world-wide stocks.

The distribution of *Phyllodactylus* seems to be explainable only by immigration from the Pacific. The weight of the distribution is on the west coast of America. Access to the Caribbean has been clearly along two routes: (i) a major one along the northwest arc, and from this to the neighboring islands and to Puerto Rico, and (ii) a less important one from Chiapas and Guatemala into the Gulf of Honduras. Many environments apparently favorable, but not easily accessible from the Pacific, remain unoccupied.

This hypothesis is in a way strengthened by a consideration of the relevant oceanic currents (Sverdrup, Johnson & Fleming, 1942: 701 seq.). The two disjunct coastal areas in which *Phyllodactylus* is found are on the bend of two major Pacific Ocean east-moving currents: the Peru Current and the Equatorial Countercurrent. The area in which *Phyllodactylus* does not exist is in the domain of the South Equatorial Current, which runs west, and on whose path are the Galapagos. Darlington (1957: fig. 7) presents a sketch map of the situation.

The only difficulty in the way of the hypothesis is the absence of *Phyllodactylus* in the Pacific islands east of the New Hebrides. (I am not considering the Galapagos, for the reason stated above, as a way station from the Pacific to South America). I have at present no explanation for its absence in Oceania, but even if we have to accept that the genus was able to cross the ocean but unable to establish itself in the islands, the hypothesis still seems to me the most tenable. Only a good taxonomical revision will indicate how many arrivals are necessary to explain the existing fauna.

The hemidactyloids look clearly towards the Atlantic, and so to West Africa. Given the well known lack of relationships between many significant segments of the African and South American faunas, especially mammals (Darlington, 1957), I do not believe that the hemidactyloid geckos are witnesses to a continuous distribution preceding continental drift. Here again I believe (with Darlington, 1957 and Kluge, 1967) in crossing over water. *Hemidactylus* is a good sailor, and has 2 endemic species in Cape Verde. In the oceanic archipelago of Fernando Noronha we have 2 endemic species of genera common to Africa and South America (*Mabuya* and *Amphisbaena*) whose distribution is obviously not, at this stage of knowledge, explainable through North American connections. Darlington (1957: 205) has discussed such cases. How far apart the continents were when the faunal movement (or movements) happened is a moot question.

An alternative explanation would be human transport. This I dismiss because none of the species involved is perianthropic, and there is too much differentiation in the interior for the available span of time.

Exactly the same reasoning applies to *Lygodactylus;* to me, the parallelism of the two cases reinforces the explanation.

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