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Remarks on the Geographical Distribution
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American Toads

by

JOSE M. CEI

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Contents

	<i>Page</i>
Introduction	3
Discussion	4
Conclusions and Summary	18
Bibliography	20

Illustrations

1. Map showing geographical distribution of the <i>Bufo spinulosus</i> group and other factors	5
2. Sympatry area on map shows subspecific divisions of <i>B. spinulosus</i> toads	6
3. South American range of the <i>marinus</i> group	11
4. Geographical fragmentation of the <i>B. granulosis</i> complex	13
5. Geographical distribution of the <i>B. typhonioides</i> complex	14
6. Geographical distribution of the Amazonian <i>B. guttatus</i> group and some barely known neotropical toads	16

Remarks on the Geographical Distribution and Phyletic Trends of South American Toads

JOSE M. CEI^o

INTRODUCTION

The genus *Bufo*, widely spread over the South American continent, is absent only in a few of the Austral Patagonian territories, in Tierra del Fuego, and on some of the Pacific coastal deserts. It appears in limited numbers in the highest Andean areas. Due to their ecological plasticity, these toads have been able to fit favorably into a great variety of environmental niches; their present trends of distribution are in accordance with the general patterns of their phylogeny and the present physiognomy of their speciation. This paper will deal with some aspects of the geographical distribution of the most important lines of the neotropical toads, bearing in mind, moreover, some of the recent contributions on the systematics and ecology of several of these forms, together with their genetic and physiological relationships.

Disregarding any previous taxonomic or historical question, a discussion of infrageneric relationships in the neotropical forms could be pointed out from Tihen's paper (1962) which deals especially with comparative osteological features. Although the studies of Noble (1931) and Davis (1936) deal with the phylogenetic relations of the Bufonidae, as suggested by any available anatomical or zoogeographic evidence, no special attempt had been made to determine and delimit the supraspecific evolutionary groupings of this polymorphous genus before reports by Blair (1963) concerning the origins and evolutionary development of the actual species of toads, particularly of the New World species. Among the most interesting conclusions of Blair's experimental contributions is that two main lines of American *Bufo* have been stressed, based on the ancient evolutionary and biogeographical history of the most precocious stocks of these Anurans. A northern line, related to some Tertiary *calamita*-like stock, could support the present relationships between the Nearctic groups: *B. boreas-punctatus* and *B. americanus-woodhousei*. A hypothetical relationship between them and the neotropical *spinulosus* complex was also suggested. On the other hand, a southern line, as an early segregation from a *melanostictus*-like stock has been postulated due to the present evolutionary trends of groups such as *valliceps* and allied forms, *canaliferus*, *coccifer*, *occidentalis*, etc. Morphological and biological affinities of these toads with the widespread neotropical *marinus* group were stressed. Such a tentative arrangement must be considered seriously from every ap-

^o Universidad Nacional de Cuyo, Mendoza, Argentina.

proach regarding the general distribution and ecology of neotropical bufonids. Moreover, it must be pointed out that assumptions taken from Blair's analysis are supported by objective evidence from genetic compatibility and experiments on interspecific hybridization.

DISCUSSION

Amphibians, although fundamentally sthenoid vertebrates, agree with both the topographic and climatic characteristics of soil and habitat, along the main lines of their geographical distribution and ecology. Dispersal of genera and species groups is thus a late consequence of the paleogeographic and paleoclimatic alternatives of the emerged lands. From such a postulation, South American toads could be apportioned into two geographically characterized areas. One of these corresponds to the great Andean embossments since the late Tertiary and Quaternary ages, the other to the lowered and eroded remains of the pre-Tertiary landscapes together with the great plains of the basins representing the hydrographic continental networks. All of them head toward the eastern or northeastern shorelines of the continent. To the first section belong those toads known as *spinulosus* complex and their allied forms (cf. "*spinulosus* group" by Tihen, 1962). In the second section there is a great number of species or species-complexes which are mostly related to the *valliceps* group proposed by Tihen (1962), both to the South American and the Caribbean sections as defined by that author. Let us consider here, separately, the physiognomical, geographical, and ecological pattern of these various categories.

The bufonids of the *spinulosus* group live in the Andean mountains from Ecuador (Loja province) to the south of Chile and Argentina (Fig. 1). Isolated or marginal populations may be observed also in the extra-cordilleran environments, as along the Chilean coasts, or in the Sierras of Cordoba, Argentina. *Bufo spinulosus*, in its broadest sense, is a polymorphic, polytypic species. Strongly adaptive, this species seems to split into geographic units when under more or less strict conditions of geographic isolation. Correct levels of biological interrelations between such units can be determined only from studies of genetic compatibility and by comparison of ethological and physiological characters.

A super-species, *B. spinulosus* Wiegmann, 1834, was first discovered by Molina among the Chilean populations in 1778, and later by Garnot and Lesson in 1828. Related species, sometimes discussed as being of sub-specific value, are: *B. trifolium* Tschudi, *B. cophotis* Boulenger, and *B. rubropunctatus* Guichenot. A further related form exhibiting peculiar features, *B. variegatus* Gunther, should be discussed here. Its widespread distribution and general tendency toward a remarkable polymorphism, together with the topographical and climatic barriers, are factors which are involved in the formation of the sub-specific divisions of *spinulosus* toads. To date, the following sub-species have been recognized from north to south (Fig. 2): *B. s.*



Fig. 1—Geographical distribution of the *Bufo spinulosus* group (s) in Andean South America. (B): channel of the Bolivar geosyncline (Eocene-Middle Miocene); (E) Entrerrian Mio-Pliocenic sea. (Dotted areas in this and following maps refer to xeric continental environments of the Chaco and Caatingas; San Francisco River).

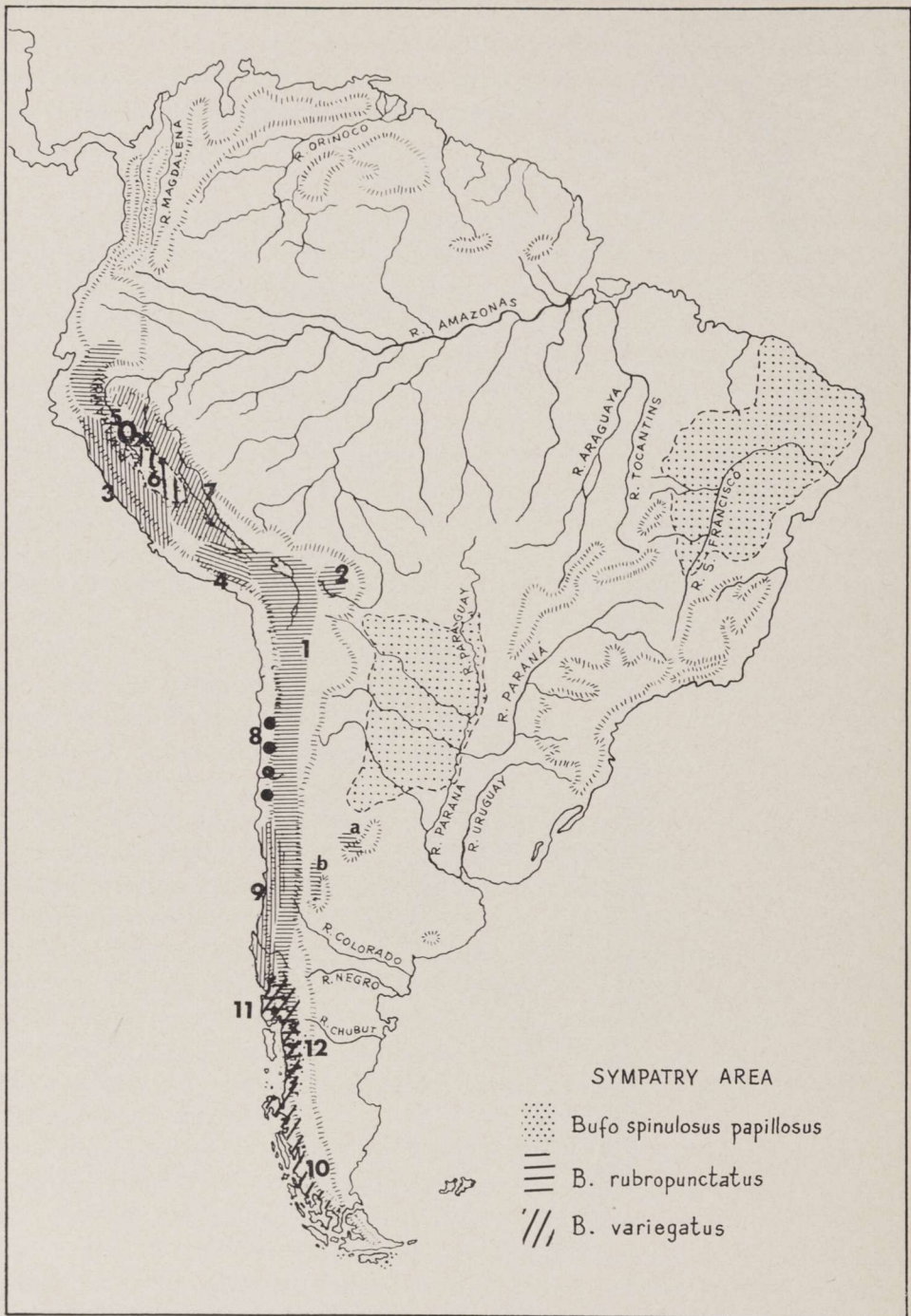


Fig. 2—Subspecific divisions of *Bufo spinulosus* toads. (1) *B. s. spinulosus*; (2) *B. s. alliperuvianus*; (3) *B. s. l'imensis*; (4) *B. s. arequipensis*; (5) (round circle) *B. s. orientalis*; (6) *B. s. flavilineatus*; (7) *B. trifolium*; (8) *B. s. atacemensis*; (9) *B. s. chilensis*; (10) *B. variegatus*; (11) *B. rubropunctatus*; (12) *B. s. papillosus*; (x) *B. cophotis*. Extra-andean populations of *B. spinulosus*: (a) "Sierras de Cordoba", and (b) "Sierras de Tunuyan."

orientalis Vellard from the high Marañon Valley; *B. s. limensis* (Werner) from the western valleys, south of Lima to Chiclayo and Olmos on the northern desert coast; *B. s. flavilineatus* Vellard from the high Central Andean plateau, between Junin and Callejón de Huaylas, up to an altitude of 4,600 meters; *B. s. spinulosus* Wiegmann from the southern Andean region of Peru, mountains of Tarapáca and Antofagasta, Chile, the Bolivian plateau near Lake Titicaca and south of La Paz, as well as in the Argentine Cordilleras; *B. s. arequipensis* Vellard from the Arequipa mountains and their southwestern valleys (Moquegua, Tarata) down to the Peruvian district of Tacna; *B. s. altiperuvianus* Gallardo from the Oruro mountains, Bolivia (3,700 meters; *B. s. atacamensis* Cei from the coastal rivers and streams of the desert of Atacama in Chile; *B. s. chilensis* (Tschudi) in the central and south-central areas of Chile, from the seashore to the Cordilleras; *B. s. papillosus* (Philippi), from southern Argentina (Rio Negro, Chubut) and Chile (from Curacautin southward).

Bufo trifolium Tschudi occurs between latitudes 7 degrees and 15 degrees south, approximately, starting at an altitude of 2,000 meters on the eastern Andean slopes up to the high Amazonian borders of the rain forest (*ceja de montana*). Vellard (1959) calls attention to its affinities with *spinulosus* and *flavilineatus*, which it replaces at the same latitude on the humid *paramos* of the Junin plateau. Its specific position is also questioned by Vellard, who calls it *B. s. trifolium* (Tschudi). According to Vellard's arrangement, all the Peruvian bufonids which belong to the *spinulosus* complex could be grouped into three morphological groups according to their skin structure and somatic parameters. *Bufo s. spinulosus* and *B. s. arequipensis* show a number of affinities, and their skins are covered at random by many cornified, conical or rosette-like warts. Another subspecific group may be identified in the large *B. s. limensis* and its eastern ally, *B. s. orientalis*, in which the majority of the warts, also irregularly distributed, are conical. A third section, strongly differentiated, is represented by *B. trifolium* and *B. flavilineatus*, covered by rounded, rosette-like warts, disposed in longitudinal series along their backs, alongside an evident light vertebral line.

Bufo cophotis seems to be a good species according to Vellard's redescription. Specimens are rare and those from Cajamarca, Libertad and Ancash (Andean Peruvian provinces) always are found between 2,200 and 2,400 meters. Its geographical distribution is between those of *B. limensis* and *B. trifolium*, but its sympatry with either of these toads has not yet been reported.

As assumed by Vellard, with respect to the intergrading border populations of Peruvian forms, a transitional zone from the southern *arequipensis* populations to the northern and eastern Chilean mountain populations could be postulated. The conditions of great aridity, prevalent perhaps since the late Pleistocene, are what determine a very irregular distribution there. In like manner, the Peruvian coast between Pisco and Ica and Camaná, and the

very dry or azoic Chilean deserts, hinder an ecological and distributional continuity of the species, which is reported from the Tarapacá valleys (Putre, Parinacota, Caquena) up to the high plateau (Puna), from the Pica oasis, the Loa river and the small streams facing the very extensive stony deserts of the Antofagasta and Atacama provinces.

From our present knowledge it is impossible to distinguish local subspecific units in the populational chain which lies alongside the Andean system for some thousands of miles, from the Puno and Parapacá mountains to the southern Argentine provinces of Mendoza and Neuquen. All of these toads are related to *B. s. spinulosus* Wiegmann, but a near subspecies, *B. s. altiperuvianus* Gallardo, in the Oruro region (Challapata, 3,700 meters altitude, Bolivia), has been described on the basis of small differences in the shape of the head and tympani. On the extra-Andean Sierras of Córdoba (Sierra de Achala, central Argentina) an isolated and poorly known population has been described, as have a few samples obtained from a small longitudinal precordilleran hill line called the Sierras de Tunuyan or Gauyquerias, south of Mendoza (altitude 1,000–1,200 meters). The presence of such extra-cordilleran relicts of *B. spinulosus* sound very interesting. It is possible that, through Pleistocene times, the range of the species could have extended eastward during a more humid and cooler climatic condition, but it is also possible that relict disjunct populations may reflect a former stage of a primeval radiation of the *spinulosus* stock.

A southernmost form, *B. s. papillosus* (Philippi) has been reinstated by Gallardo for some of the Argentine and Chilean populations adapted to the moisture of the transitional woods of the *Austrocedrus* and *Nothofagus* associations. It is difficult to establish its northern limits with *B. s. spinulosus* in Argentina, and *B. s. chilensis* in Chile. The latter, contrary to Gallardo's statement, does not exist in Argentina. Southward, its area partially overlaps the area of the forest toad *rubropunctatus*, the specific status of which is well supported, its general features being at first glance strongly reminiscent of Californian *B. exsul*. Likewise, in the *Nothofagus* forest, *B. variegatus*, the most diversified species of the *spinulosus* section is found. This species is outstanding because of its structure and the position of its parotids, but due to its pigmentary pattern, strikingly similar to *B. flavilineatus-trifolium*. Also, the similarity of some of the metabolic properties of the skin of *trifolium* and *variegatus* must be stressed (Cei and Erspamer, unpublished data), in spite of the extreme geographic disjunction of these toads. This is seen in the enzymatic activity leading to the advanced methylation of the amine tryptophanic derivatives. Lack of sulconjugase activity is remarkable both in *B. variegatus* and *B. trifolium* as opposed to the uniform amine spectra of all other *spinulosus* toads examined so far.

A first analysis of the present dispersal suggests the *spinulosus* section as the only bufonid line following the late Tertiary Cordilleran epeirogenic uplift. Speciation seems to be stronger at the borders of its distribution (*B. tri-*

folium-flavilineatus and *B. cophotis* in the north; *B. variegatus* and *B. rubropunctatus* in the south), but its genetic compatibility is probably quite different also among the most remote and geographically separated populations of *spinulosus*. Some of the adaptive trends, such as the loss of a mating call, the resistance to dryness, skin warts, etc., are widespread. Yet, the high populational differentiation agrees with a prolonged evolutionary process covering, especially, the Pliocene and post-Pliocene history of Cordilleran morphology and climatic changes. No species of *Bufo* other than *spinulosus* lie between the Andean Cordilleras and the Pacific coast, southward from latitude 7 degrees south. Moreover, they are the only toads in the Valdivian forest, a truly relict environment of Miocene features, as shown by the Pichi Leufú flora studied by Berry (1938). Recent synopsis of the key geological events for American herpetofauna, as in Stuart's (1966) or Savage's (1966) discussions, emphasize a separation between nuclear Central America and South America from Eocene to Pliocene, and a reconnection of the two areas through the isthmian link from the early Pliocene onward. But there was also an uplift of the continental highlands from the Miocene to present times, together with increasing xeric conditions along the Pacific coast during Pliocene and Quaternary times. Such a basic historical factor is very significant in assuming the origin of Andean herpetofauna or a critical interpretation of highland dispersal routes, as in the case of bufonid anurans.

If the *spinulosus* Andean complex could admit backing a very ancient northern relationship as its general *calamita*-like or *boreas*-like features might suggest, its dispersal route would then be extant as early as in Paleocene times, or even as late as in the Middle Pliocene. The first assumption is, of course, completely hypothetical, although the independent evolution of many South American elements during the Eo-Oligocene and Miocene is well supported by paleontological findings (Schaeffer, 1949; Chaffee, 1952; Tihen, 1962). Moreover, the controversial question of a Paleocene isthmian link between the western "paleozoic" borderland and the Cordillera Central of Colombia remains to be answered. Besides the sinking of the western borderland in the mid-Miocene and the emerging Cordillera Central, another very important paleogeographic factor must be stressed for the northwestern South American evolution. A broad channel of the Bolivar geosyncline, which started during the Eocene period and extended from the Caribbean Sea to the Gulf of Guayaquil, disconnected the emerged South American lands, from the Lower Oligocene to the Middle Miocene (Stuart, 1966).

On the other hand, a Pliocene invasion by the two-way isthmian dispersal route is countered by the present lack of intermediate *spinulosus* populations from Mexico and Central America to the Ecuadorian mountains. Blair, however (personal communication), regards *B. bocourti* of Guatemala as providing such an intermediate population. Otherwise, a gap in the *spinulosus* distribution seems to exist in the emerged lands corresponding to the Cordillera Central of Colombia and the North Andean syncline, although fossil

remains of *marinus*-like toads have been reported from the La Venta fauna of Colombia (late Miocene of Magdalena Valley, Huila). From Pliocene times onward, the great geological activity, volcanism and the consequent topographical barriers, and the glaciations with their biocenotic effects, may have been the prevalent conditions which affected dispersal movement. Conversely, they may have been the very active factors in provoking speciation and populational isolation in a former stock of indigenous elements. Similar remarks could be made regarding another significant Andean genus, *Telmatobius*, whose distribution almost overlaps that of the *spinulosus* group.

Almost all of continental South America, east of the Cordilleras, is covered by toads of the *marinus* group. A true Amazonic form, *B. marinus marinus* (Linné) penetrated Central South America, probably after Pliocene connections were made, or originated there as Blair (personal communication) now believes. Estes and Wassersug (1963) stressed neotropical features of *marinus*, discussing the systematic status of a fossil from the upper Miocene of Colombia (Honda) (Fig. 3). A smaller form, *B. m. poeppigi* (Tschudi) replaces *m. marinus* on the eastern Andean slopes, crossing the Cordilleras between latitudes 0 degrees and 7 degrees south, down to the equatorial Pacific shores. This border distribution of *poeppigi*, going southward to the Bolivian *yungas*, recalls other peripheral forms of this species complex, such as *B. rufus* Garman from the *planaltos* of Brazil (Goyaz, Minas Gerais), and *B. arenarum* Hensel from the south of Brazil, Uruguay and Argentina, and overlapping *poeppigi* northward, in the Bolivian Plateau (Cochabamba). These peripheral species of the complex are adaptive forms, capable of tolerating environmental dryness, and ranging along the Cordillera uplands up to remarkable altitudes, as *B. arenarum* at an altitude of 1,500 or more meters above sea level in western Argentina, or *B. m. poeppigi* in the northern Peruvian highlands. Strong populational differences have been reported regarding *B. arenarum*, many subspecies of which have been recognized by Gallardo (1965) as, for instance, *B. a. arenarum* Hensel from Rio Grande do Sul, *B. a. platensis* (Espada) from the Pampean belt, and *B. a. mendocinus* (Philippi) from the western xeric Argentine territories. These are perhaps merely subjective interpretations of a physiological adaptive polymorphism of the species. Peripheral forms and their speciation, at any rate, probably agree with an ancient stage of a continental radiation of some undifferentiated *marinus*-like stock of neotropical toads. Their moderate overlapping in some of the peripheral areas of the *spinulosus* range may signify a relatively recent invasion of Andean mountain environments.

The humid forest belt of the eastern Brazilian Serras contains another characteristic form, *B. ictericus* Spix (Fig. 3), so closely allied to *B. m. marinus* that its subspecific status has frequently been discussed. *Bufo ictericus* is a forest toad, connected through its mesic trends to the Amazonian form, from which it is presently separated by the broad xeric central zone of the *monte* and *caatingas* extending over the southern Chacoan plains (Santiago

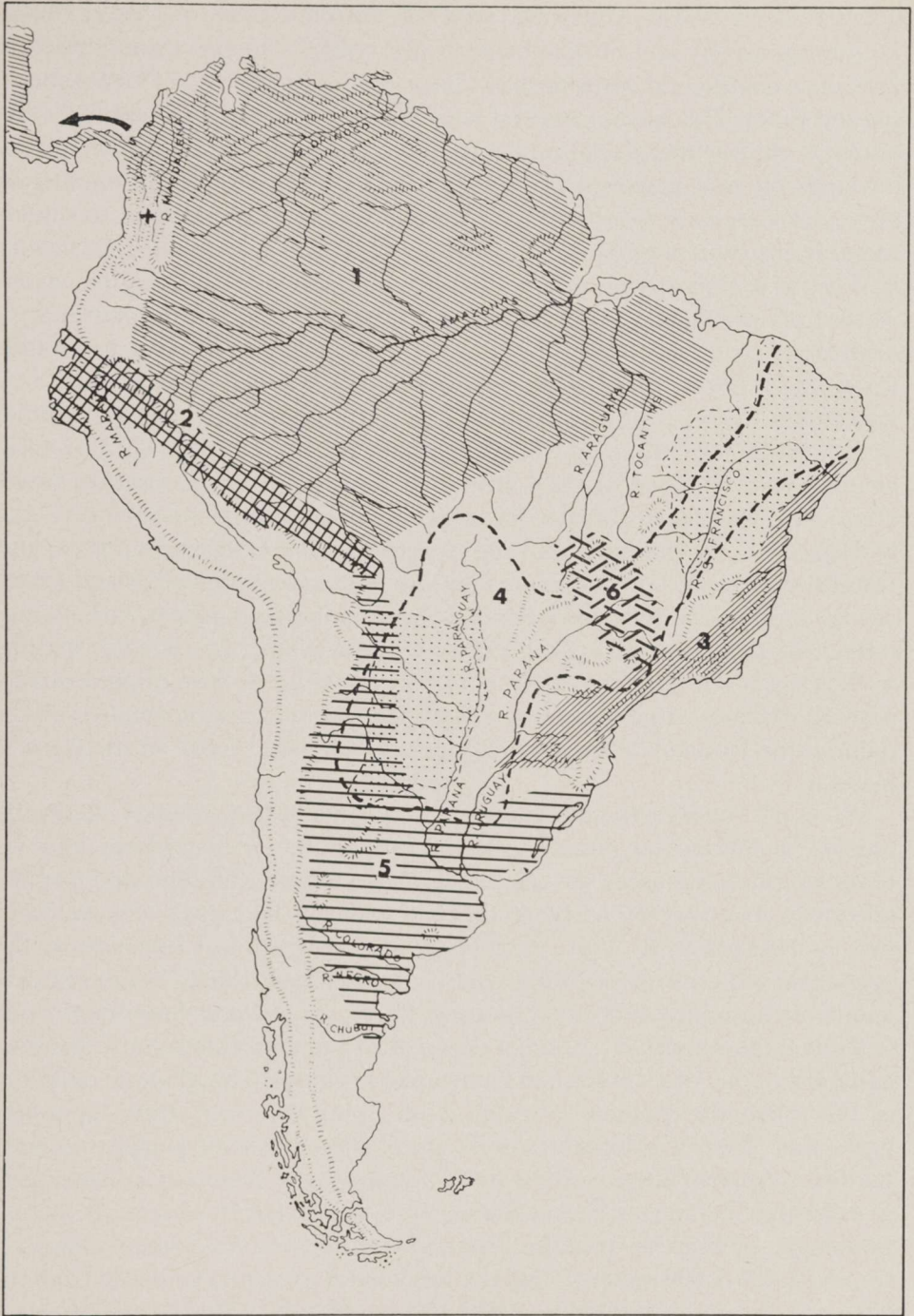


Fig. 3—South American range of the *Bufo marinus* group. (1) *B. m. marinus*; (2) *B. m. poeppigi*; (3) *B. ictericus*; (4) *B. paracnemis*; (5) *B. arenarum*; (6) *B. rufus*. (Plus mark indicates fossil remains of *B. marinus* in upper Miocene of La Venta, Colombia).

del Estero, Santa Fe, Argentina) and the northern coast of Ceará, Brazil. Increasing aridity and development of the typical climatic communities of that xeric continental corridor, have been occurring from the Pleistocene to present times. This species evolved with the changing climate, flora and morphology, during the glacial and interglacial periods. These mediterranean lowlands are thus responsible for a very active speciation, and a number of xeric forms are now reported from Chacoan territories, equivalent to similar mesic forms from neighboring environments. This is true for the *marinus* as well as for the *granulosus* group (Caribbean section of Tihen). *Bufo paracnemis* Lutz precisely covers Chacoan and Caatingas areas, with some gaps in central eastern Brazil. Such a distribution is also followed by some geographical forms of *granulosus*: *B. g. major* Muller and Hellmich in the Chaco; *B. g. granulosus* (Spix) in Rio Grande do Norte, Pernambuco, Bahia and Ceara; *B. g. lutzii* Gallardo from the San Francisco River basin (Fig. 4). This xeric element very likely occurs as a late specialized stage in the *marinus* speciation. *Bufo paracnemis* breaks the actual distribution of all mesic forms—the widespread *B. m. marinus* from the Amazonian and Guayanian basins, and the eastern *ictericus*. In Sao Paulo and Rio de Janeiro, *paracnemis* and *ictericus* are found, according to Cochran (1955), in the same places without any intergrading, but occupying different ecological niches, i.e., flowing streams in the case of *ictericus*, but drier mountain ridges in the case of *paracnemis*. Also in Misiones, Argentina, where they are sympatric, *paracnemis* is abundant on the Paraná border, as is *ictericus* in the humid forest of the Central meseta.

When we consider the really conservative area of the so-called “Guayana Shield,” a continental radiation of three other species-complexes may be observed; these probably are related also to some non-differentiated tropical ancestors, in a very broad sense to some valliceps-like stock of a southern line, as referred to by Blair. A phyletic and geographical radiation of the *typhonius* and *granulosus* groups could be pointed out. Finally, some scarcely known western elements could be considered: the *guttatus-blombergi* toads from the high Amazonian Andean slopes of Ecuador and southern Colombia, eastward to the Venezuelan and Guayanian lowlands. The phyletic radiation of the *typhonius* complex (Fig. 5) is an Amazonian one. *Bufo typhonius typhonius* (Linné) is the central widespread form, but some peripheral forms border its tropical range, such as *B. typhonius alatus* Thomassinot in Venezuela, *B. ockendeni* Boulenger, *B. inca* Steineger, *B. leptoscelis* Boulenger, *B. fissipes* Boulenger, all of them from the Peruvian and Bolivian Amazonian mountain slopes (1,400–2,000 meters), and the localized *B. quechua* Gallardo from the Chaparé, Yungas of Colombia, 2,600 meters (Bolivia). These toads are similar and well characterized by their hypertrophied cephalic crests or the curious hyperthelia of their snouts. The most remarkable ones are those few localized and rare species, such as *B. dapsilis* Myers and Carvalho of the Amazonian basin (Benjamin Constant), *B. coeruleosticus* Gunther (Ecu-



Fig. 4—Geographical fragmentation of the *Bufo granulosis* complex. The following forms have been checked: (1) *B. humboldti*; (2) *B. barbouri*; (3) *B. beebei*; (4) *B. merianae*; (5) *B. natiereri*; (6) *B. goeldi*; (7) *B. minor*; (8) *B. mirandariberoi*; (9) *B. granulosis*; (10) *B. lutzii*; (11) *B. major*; (12) *B. azarae*; (13) *B. fernandezae*; (14) *B. d'orbignyi*; (15) *B. pygmaeus*. (Note sympatry area along the Parana River).



Fig. 5—Geographical distribution of the *Bufo typhonius* complex. (1) *B. t. typhonius*; (2) *B. t. alatus*; (3) *B. ceratophrys*; (4) *B. dapsilis*; (5) *B. ockendeni*; (6) *B. inca*, *B. leptoscelis*, *B. fissipis*; (7) *B. quechua*; (8) *B. crucifer*; (9) *B. sternosignatus*.

dor), and *B. ceratophrys* Boulenger from the Amazonian and Orinoco Basins. The *B. typhonius* complex is probably replaced in the eastern Brazilian territories by the less differentiated *B. crucifer* Wied and its scarcely defined subspecies. *Bufo sternosignatus* Gunther also seems to be a Venezuelan toad close to this group (or to the *granulosus* group), but so far, hardly known. Porter (1964) places it as a synonymic species of *B. valliceps*. *Bufo sternosignatus*, however, is not the only one of a number of neotropical bufonids lacking an up-to-date and adequate screening or recognition. To this uncertain and still museologic category should be added *B. ocellatus* Guenther from Minas Gerais, *B. intermedius* Guenther, and *B. manicorensis* Gallardo from Amazonia, Rio Madeira (Fig. 6).

Perhaps the extreme degree of geographical fragmentation is exhibited by the *granulosus* complex, appearing as a widespread and probably ancient stock closely related to the highly differentiated *peltocephalus* complex from the Caribbean Islands. Its affinities with the *valliceps* or southern line are hinted at by some of their morphological features, such as their cephalic crests or cranial structure, as well as by a relatively high generic compatibility with some of the representative forms of such a bufonid group, as *B. arenarum* or *B. valliceps* (Blair, unpublished data). A central species is recognized by Spix (1824) and in some recent contributions many subspecific geographical units have been reported (Gallardo, 1965; Bokermann, 1966). It is likely, however, that with a further and more adequate screening of the genetic compatibility and eco-physiological relationships between these so-called subspecies, specific status of some of them will be indicated. Gallardo (1965) emphasizes a remarkable agreement between distributions of *granulosus* subspecies and continental hydrographical systems, and some insular endemisms, as *B. g. barbouri* Gallardo from Margarita Island in Venezuela. In the Magdalena and Orinoco Basins, *B. g. humboldti* Gallardo and *B. g. beebei* Gallardo have been reported, as has *B. g. merianae* Gallardo in the Guiana region. Furthermore, Bokermann (1966) describes an additional form, *B. g. nattereri* n. sp., from the Roraima Mountains near the Guiana-Brazilian frontier where, he says, *B. g. humboldti* also exists; in this case, *B. g. humboldti* probably would be sympatric with *B. g. merianae* and *B. g. nattereri* from the same biota. *Bufo g. goeldi* Gallardo belongs, then, to the Amazonic basin, while *B. g. miranda-riberoi* Gallardo corresponds to the Aguaraya-Tocantins Basin, and *B. g. minor* Gallardo to the upper Beni region. The distribution of the xeric central forms, *B. g. major*, *B. g. lutzi*, and *B. g. granulosus*, has been pointed out, while a further subspecies (*B. g. azarai* Gallardo) is also indicated from the Paraguay Basin (Sierras de Maracayu and Amambay, Primavera). But east of the *monte* and *caatingas* other forms extend, which we should like to consider as distinct species, according to many kinds of biological evidence. Such forms now seem to be well separated from the *granulosus* toads of the *granulosus-major-lutzi* group which show, from the same observations by Gallardo, a number of common and significant



Fig. 6—Geographical distribution of the Amazonian *Bufo guttatus* group and of some uncertain or little known neotropical toads: (1) *B. g. guttatus*; (2) *B. g. glaberrimus*; (3) *B. blombergi*; (4) *B. ocellatus*; (5) *B. manicorensis*; (6) *B. haematiticus* and *B. coniferus*. (Arrows indicate the two-way dispersal routes by the Tertiary isthmian link).

characteristics (Cei and Roig, unpublished paper). Eastern forms are *B. fernandezae* Gallardo, *B. d'orbignyi* Dumeril and Bibron, and *B. pygmaeus* Myers and Carvalho. *Bufo fernandezae* and *B. pygmaeus* are sympatric on the western borders of the Paraná River, between Resistencia and Santa Fé, but allopatric over a wide range (Fig. 4). These toads are well differentiated in the area of sympatry due to their physiological-biochemical characters (seroproteins, hemoglobins) and ethological features (warning and mating calls) in addition to their morphological characteristics. *Bufo fernandezae* and *B. d'orbignyi* probably have a greater affinity to each other, possibly at a subspecific level, than to *major* and *pygmaeus*, with which they are sympatric.

If specific status could be proven for these members of the *granulosus* complex as well as for other populations from the widespread range of these toads (such as *B. humboldti*, *B. nattereri*, and *B. merianae* from Roraima), a striking similarity with the speciation and evolution of *marinus* and perhaps *typhonius* complex then would be obvious. The same would be true if they exist in the western zone, in Orinoco and the Amazonian basins, as other specific and subspecific allopatric complexes. We are actually concerned with a number of mesic forms distributed about the high and low Amazonian basin and along the Orinoco and Guiana range, facing a number of mesic forms from the humid eastern Brazilian range, both cut off by the xeric corridor from the south to the northeast and its adaptive specialized elements.

This parallelism is very significant. If the common ancestors of such a diversity of phyletic lines are believed to represent early and generalized relationships between North and South American continents, joined by an ancient connection of not later than early Tertiary, a quite similar early separation of the actual diverging lines could be stressed. This would agree with such an extended independent evolution as supported by these repeated parallelisms. Ecological factors influence distributional trends, especially after the Pliocene isthmian connections. The invasion of Central America by *B. granulosus* or *B. typhonius* toads is, surely, a limited and slow one in comparison to a distribution such as that of *B. marinus*, which has subspecific differentiation northward to Mexico (*B. m. horribilis* Wiegmann).

Dissimilar distributional and phyletic trends are exhibited by the soft-skinned toads of the *guttatus* group, which lack cephalic crests. This group is represented by *B. g. guttatus* Schneider, *B. glaberrimus* (*guttatus glaberrimus*) Gunther, and *B. blombergi* Myers and Funkhauser, a giant form from Ecuador and Colombia. Large toads such as *B. glaberrimus* and *B. guttatus* are distributed within the high basins of the Amazonian rivers in the Orinoco and Guiana shield. The giant form, *B. blombergi*, has a distribution extending from Narino, a southern Colombian province, toward the Pacific Colombian coast (Fig. 6). On the Pacific shores, in Choco, from Costa Rica and Panama, northward to Cartagena on the Caribbean Sea, *B. haematiticus* Cope is found. This species is morphologically related to *B. guttatus* and is followed

in its dispersal by a Central American element, *B. coniferus* Cope. Blair (1966) has demonstrated that *B. coniferus* belongs in his *valliceps* group. The two-way dispersal route established in the upper Tertiary is here evident, but the *B. guttatus* group suggests a real ancestral physiognomy of tropical forest element, and its center of dispersion probably was in the Guiana lowlands, extending during the Middle Tertiary as far as the borders of the emerging lands of the geosynclines of Colombia.

CONCLUSIONS AND SUMMARY

The present distribution and ecological trends of *Bufo* in South America are, fundamentally, the consequence of major geological events and paleogeographic and paleoclimatic changes, acting since Mesozoic times on the continental landscapes and biocenotic communities. Ancient relationships with their common Nearctic ancestors from the northern and southern lines could be supported by the many kinds of biological evidence, such as genetic compatibility in interspecific crossing (Blair, 1961, 1963, 1964, 1966) or serological relationships (Cei and Cohen, 1965), but a reconstruction of the connecting routes—undoubtedly previous to the Cenozoic separation by the Panamanian portal (Paleocene?)—is still a controversial question. Thus the tectonic history of the northwestern section of South America since Mesozoic times and paleogeographical relationships between the emerging Cordillera lands of Colombia and nuclear Central America are under discussion.

Because of their evolution, two fundamental groups of toads stand out. *Bufo spinulosus* and its allies seem to have followed the Andean orogenesis, reaching the most impressive specialization for life in the highest of environments, and accompanied in such biotopes only by such leptodactylids as *Telmatobiinae* or *Pleurodema* and, occasionally, by some hylids such as *Gastrotheca* in Peru. Speciation of this group, at any chronological stage, corresponds to the evolution of the Cordilleran topographic units, acting as geographical or ecological barriers for the isolation of populational genetic systems. Species of the *B. spinulosus* complex are, moreover, the only existing bufonids from the Valdivian forest biocenotic communities, a Miocene relict now in equilibrium since its post-glacial recuperation. Dispersal of *spinulosus* north of Ecuador may have been countered by paleogeographical factors. A comparison may be carried out between the complete lack of the species north of Ecuador and the unstable Cenozoic history of northwestern South America and the broad channel of the Bolivar geosyncline, which was completely flooded from the lower Oligocene until the Middle Miocene “when sediments from the now-high western Andes began filling it” (Nygren, 1950; Stuart, 1966). It is possible that the bufonid branch corresponding to the *B. spinulosus* complex could have undergone its phyletic radiation from some austral, perhaps Patagonian, center (*B. edentatus* (Schaeffer), Tihen, 1962), toward the Cordilleran front. The radiation of this branch

probably was limited to the northeast by Cenozoic events such as the Molassa or Enterrian Mio-Pliocene seas, and later by increasing aridity.

Neotropical bufonid stocks in some very ancient relationships with *B. valliceps*-like ancestors are *B. marinus*, *B. granulatus* and *B. typhonius* complexes, probably *B. crucifer*, and perhaps somewhat farther off, the *B. guttatus* complex. A form from the last-named, *B. blombergi*, has been included by Tihen in his South American section, together with *marinus* and *crucifer*, but remarkable differences between them have been repeatedly stressed. A more attentive analysis of the real relationships between the *B. guttatus* complex and *B. haematiticus* should be welcome. Tihen, when considering *haematiticus* as a peculiar group having relict features, emphasized some of its affinities with the *valliceps* group and likewise with the African toads from the *regularis* line.

All of these neotropical specific complexes, already well established since Middle Tertiary times (Estes and Wassersug, 1963), can be considered as probably having evolved from a primeval center of radiation, possibly the stable "Guiana shield". Current trends of these forms toward more mesic environments agree with past and present patterns of distribution, leading from a peripheral zone of speciation in the high Amazonian forest (as stressed by such forms as *peoppigii*, *minor*, *ockendeni*, *fissipes*, *leptocelis*, *inca*, *quechua*, *glaberrimus*, *blombergi*, etc.) to a set of local forms from the humid, conservative plateau of eastern Brazil. A very early emergence of the Brazilian shield also is indicated. The striking disconnection due to the central and northeastern xeric post-Pliocene zones (*monte* and *Caatingas*), provides a number of highly adaptive forms, very likely of recent speciation (*B. paracnemis*, *granulosus granulatus*, *granulosus major*, etc.). Southern *arenarum* toads show up as peripheral elements of a former wide radiation, stressing a great ecological adaptiveness and probably less differentiated in agreement with some relative position of phyletic intermediacy, directly connected to ancestors of the present South American groups, and the *valliceps* group itself. They also overlap *peoppigii*, *paracnemis*, and some representatives of the *B. granulatus* complex. By courtesy of Blair (unpublished data, personal communication) we may add that preliminary testing indicates a striking genetic compatibility (in some cases up to the apparent fertility of the F₁ hybrid offspring) between *B. arenarum*, *B. paracnemis*, *B. granulatus*, and *B. valliceps*. Also in some crossed precipitin serological tests we found very high percentages of homoheterologous reactions between *B. paracnemis*, *B. arenarum*, and *B. marinus* as well as between *B. paracnemis* and *B. valliceps*. On the other hand, all of these forms show, in the same tests, the most remote serological distance from elements of the "northern line", such as *B. boreas* or *B. woodhousei*, and likewise from *B. alvarius*, and from *B. spinulosus* toads, both from Andean Mendoza, Argentina, populations or from the Peruvian form, *B. limensis*, near the Pacific shores on the farthest border of its distribution.

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