The effect of Altitude upon the Distribution of Mexican Amphibians and Reptiles.

By

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With 6 figures in the text.

It is as well to confess at once our ignorance of the detailed working of the many factors which are connected with a change of altitude. It implies temperature, atmospheric pressure, and according to the locality saturation, cloudbelts, wind, radiation and insolation. About the effect of varying pressure upon terrestrial animals we know next to nothing, whilst we are beginning to correlate the influences of some of the other factors, notably temperature. If therefore we introduce altitude as a factor in distribution, we draw our eventual conclusions without knowing which of the subfactors of altitude are the determining agents.

Altitude and longitude can compensate each other. As the annual mean temperatur decreases 0,5° C with every 100 m elevation, and 0,75° C with every degree of latitude, 10 degrees of latitude should be compensated by 1500 m elevation. Thanks to the continuous and rather steady rise of the great plateau of Mexico from North to South, this theoretical compensation works remarkably well.

A striking example are the following data:

	Lat. N.	Altitude	Mean annual Temp.
Chihuahua town	28° 38′	1450 m	18,2° C
Mexico town	19° 26′	2277 „	15,5° C

The calculated and the observed mean temperatures differing only about 0,1 of a degree! Nevertheless the respective faunas and floras of these two places are by no means identical nor living under the same conditions, because of the different pressure; further the Northern parts are droughty, the annual scanty rainfall being concentrated into a few irregular downpours, whilst the Southern part of the plateau has a regular wet season with considerably more rain; again the month of May is, in the North the time of excessive heat, when storms of dust rage, often for several days, whilst in the Southern part of the plateau such excesses are much rarer. The Atlantic or Gulf side is hot and moist, the Pacific hot and much drier.

It may therefore be doubted whether it is worth trying to draw conclusions from the altitudinal distribution of a Fauna. But Mexico is a favorable country for such studies thanks to its almost unique geographical conditions. For our purposes, and as a geographical entity, it ends as the Isthmus of Tehuantepec. The whole country is a broad-based southward extension of North America, a narrowing peninsula, the greater part of which is taken up by the obliquely slanting plateau, fringed, especially in the South and West by high ranges of mountains, and sloping down sharply to East and West, leaving an Atlantic and a Pacific long strip of low Hotlands. The Southern portion is complicated by a coast range. The Hotlands are quite tropical in character at the Isthmus, 17° N. Whence they extend imperceptibly into Texas, and in the North West up to 32° N assuming gradually subtropical features.

Thus it comes to pass that every variety of climate exists in Mexico within short distances. Hot and moist, or hot and dry lowlands, to temperate and cold plateaux and snow capped mountains. And as Mexico lies well within the tropical belt, it is easy to get into and out of the various climates, easy not only for the components of the fauna and flora but also for the naturalist who wants to investigate them.

Further, as I have shown in detail (The distribution of Mexican Amphibians and Reptiles, in: Proc. zool. Soc. London, 1905, p. 191—244) Mexico is the meeting ground of two of the fundamentally most distinct faunas and floras, the Nearctic and the Neotropical. The first has got a great lead Southwards by following the plateau which for more than one thousand miles so effectively counteracts the decreasing latitude by its steady rise. The host of Neotropicals in their northward spreading have surged against the wedge of this

plateau and were divided into an Atlantic and a Pacific branch, which eversince, strangers in a new country, have remained separated from each other and are now more and more differentiating. A few, comparatively few, of these Southerners have climbed onto the plateau and have found a footing there, whilst many more Northerners have descended from it into the Tierra caliente, some by the Atlantic, others by the steeper Pacific slope, and these also, separated as their descendants are, demonstrate the old maxim that Si duo faciunt idem non est idem.

But there is a third element, neither Neotropical nor Nearctic, namely the old indigenous Sonoran stock, an assembly difficult to discern and to handle. We shall not be far out, if we assume 1) that an older Sonoraland extended much further West, including not only what is now the narrow peninsula of Lower California at a time when Mexico to the East of the Western Sierra Madre was not yet in existence, but also land of which the Tres Marias and the Revilla Gigedo Islands are remnants. 2) That most of the present Nearctic fauna and flora are compounds of those of the old Sonoraland, and the Eastern Appalachian land-complex, with further Northern additions. 3) That whatever the extent of old Sonoraland, it must have had a coast, therefore comprising some Lowland conditions, probably tropical; it must also have been standing out very high because so much of the present Mexico to the East of it is covered to great depths with continental debris which must have come from somewhere in the West. In fact the whole plateau between the Eastern and Western Sierras Madres has a deep bottom of cretaceous Limestone, like the Eastern Sierra itself, and this immense depression has been filled and levelled up with comminuted debris, burying all but the outstanding tops of isolated mesas, hills or whole ridges of mostly marine origin, which nearly everywhere form the many-tinted far off boundaries of otherwise seemingly interminable plains. 4) That this Sonoraland may have been connected with South America, but this point we need not argue out; suffice it to say that a land-connexion existed between North and South America within the cretaceous period, and that it is equally certain that this connexion did not pass over the present bulk of Mexico.

The following investigations are to a great extent a continuation of those published in Proc. zool. Soc. 1905. There about 250 species of Mexican Amphibia and Reptiles were dealt with, because I was

satisfied with sorting them roughly into six groups. Those which are found only in the cool or cold regions; those found in these and in the temporate zone; in the cool, temporate and hot zones; in the temporate zone only; in the temporate and hot; and lastly in the hot zone only.

The lines of demarcation are quite arbitrary. The Hotlands extend, according to the practical usage of the Mexicans up to about 3000 ft., while everything beyond 7000 ft. or 2000 m can safely be considered within the cool zone. 2000 m of altitude corresponds with a lowering of the annual mean temperature of 10^0 Centigrade, a difference equal to that prevailing between London and Algeria, or New York and New Orleans.

For the present paper I have endeavoured to compile a list of those species of which the range of altitude may be considered as tolerably well ascertained, say within 1000 feet or 300 meters. In addition to my previous journeys I have since spent six months from April to September 1008 in the State of Chihuahua, visiting the Western Sierra Madre of the Tarakumare, and chiefly in the State Michoacan with such attractive and varied features as the hot depression of the Balsas basin with the wonderful Jorullo volcano, the delta of the Balsas, and the mountain of Tancitaro which rises to 13000 feet above the level of the sea. — It was not easy to collect the data and the total member of species falls short of 100. It could have been rounded up to 100 by the addition of the Crocodile, *Caiman*, and a few species of *Cinosternum* which had been omitted accidentally, but frankly I felt uneasy that such a round number might look suspicious and after the endless collations and calculations had been made and began to yield such unexpectedly good, reasonable results, I feared that additions might not be free from bias.

Although my own personally collected material comprises about 150 species, I do not feel sure about the range of more than 56 to 60 of these, less than half! SUMICHRAST (in: Arch. Sc. nat., 1873, p. 233—250) has published a paper on the distribution of snakes in South Eastern Mexico and he is the only one who has paid special attention to this matter. I had therefore to resort to the localities as reported in the literature, in many cases not at all a safe guide, fairly reliable only when the species had been reported from many localities, or by such careful collectors as the veteran DUGÈS of Guanajuato or Dr. MEEK of Chicago. Far too many species are known from a few localities only and had therefore to be left out, also

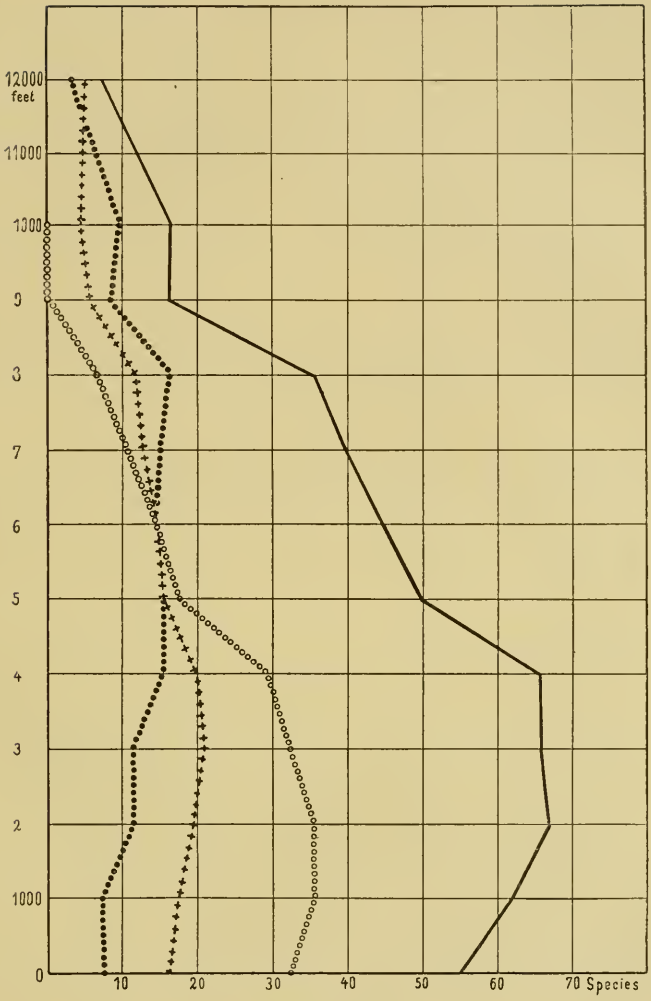

Diagram No. I.

Showing the number of species occurring at the various altitudes.

Black, unbroken line = Total number of species.
Black, dotted line = Nearctic species.
Black, crossed line = Sonoran species.
White-circled line = Southern species.

those the reputed localities of which I have sufficient reasons to consider erroneous. Thus it has come to pass that the total available material of perhaps 350 species had to be sadly reduced. By thus

drawing attention to the defective state of our faunistic knowledge of the country, future naturalists may be induced to amend it.

It may seem unwarranted to expect conclusive results from so small a number as 94 species. However as they were not selected but simply happened to be those about the altitudinal range of which I could get satisfactory data, the statistical curves which they yield, appear so unbroken and free from vagaries that this cannot well be merely accidental, but must be due to the whole list being fairly representative. Only in one point they must be wrong. The number of exclusively Hot-country species, chiefly "Southerners" is relatively much greater than represented (cf. especially Diagram III, and also p. 229, with diagram in: Proc. zool. Soc. London 1905) and it is these Lowland species about the range of which we know least. Lastly many of them seem to be restricted to the South Eastern part of tropical Mexico, at the Isthmus, therefore hardly representative.

It cannot be expected that all the results discussed in this paper are more than tentative. Some, I trust, will be contested, which may mean progress [1]), as they can be contested only upon

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1) The following statement (in: Proc. zool. Soc. London, 1905, p. 196) has produced a most valuable result, thanks to Prof. P. P. Calvert. ‚Altitude is supposed to be all-sufficient; but this is a great mistake, since it conveys nothing without further information. For instance, 2000 feet on the Atlantic slope means typical tropical hot-country vegetation, while on the Pacific side (e. g. Oaxaca and Guerrero) the same elevation implies pine — and oak forests, with a character devoid of tropical fauna and flora . . . Chilpancingo 4100 ft. in Guerrero has a much cooler climate, with nothing tropical about its vegetation, than Oaxaca, 5060 feet, or even Orizaba at 4027 feet, which is in many respects subtropical." The above has been taken by Calvert as an "assertion of the existence of a much cooler climate on the Pacific, than on the Atlantic side of Mexico at almost the same elevation". Although nothing was further from my mind than such a sweeping assertion, I own to having expressed my meaning badly, namely that the same elevation may produce different effects on the two slopes; further information about probable factors, the different amount of drainfall was mentioned on p. 237 – 239. The term "tropical" should not have been used in two senses, or in such a loose sense as synonymous with luxuriant, in the case of the Atlantic slope. Tropical vegetation is, in Mexico as elswhere, luxuriant (hot and moist climate) or xerophile (hot and dry). At least I should have said that on the Pacific slope the same elevation implies [sometimes] pine and oak forests, with a character devoid of the luxuriant character of the Atlantic slope. The want of clearness was exaggerated by passing next on to differences of temperature at

further data hitherto not available, at least unknown to me. If the whole material were at our command, a solution would bid fair to be possible upon the lines suggested and followed in this paper. The problem is a real one, because a country situated as Mexico is, has received and differentiated its fauna in reasonably traceable logically understandable ways, not by whim of accidents or haphazard dispersal. Of greater importance is the question whether my method is applicable to other classes of animals and to other parts of the world.

Species arranged according to the amplitude of their range in feet.

(Diagram No. II.)

The Curve is so good that it justifies the attempt of such an arrangement. Very few species have a range of more than 10000 feet and equally few are restricted within 1000 feet; neither of which facts is surprising. The majority have a range of 4000 feet, which is an excellent mean since it shows that most species have an amplitude a little larger than that by which the Mexicans popularly divide their country into the three climatic zones of Tierra caliente,

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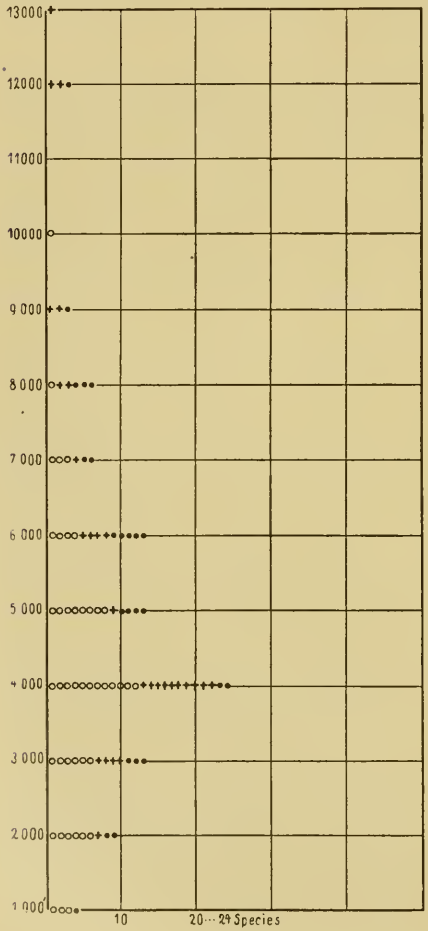
the same altitudes, and using the term tropical in its proper sense, in opposition to subtropical and temperate.

Prof. CALVERT has been stimulated by my misunderstood assertion to compile a "Collection of mean annual temperatures for Mexico and Central America" (in: Monthly Weather Review, Vol. 36, No. 4, p. 93—97, April 1908, Washington, DC.). This laborious and most useful list gives the latitude, altitude, and mean annual temperature of some 120 Mexican places. He himself has travelled extensively in that country and has laid particular stress upon the respective temperatures in his admirable account of the Distribution of the Dragonflies, in: Biologia Centrali-Americana, vol. Neuroptera, 1908. — In the paper quoted above he comes to the important conclusion that a given mean annual temperature reaches farther north and to a greater elevation on the Pacific than on the Atlantic slope of Mexico. No doubt he is right, but mean annual temperatures are queer things, because the same figure may to composed of violent extremes or of small variations. Nevertheless Chilpancingo has a much cooler climate because it is windswept and bleak, than Orizaba, or even Oaxaca which, by the way, is on the Pacific side. In 1908, when crossing the Sierra madre, or coastrange, of Michoacan, I was again struck with the non-tropical, rather temperate looking aspect at 3000 ft. elevation, for instance at Carrizal, and on exposed parts even down to almost 2000 feet.

T. templada and T. fria, respectively up to 3000, 6000 feet and beyond, above sealevel. A 4000 feet range makes an obvious difference everywhere; a species centred in the Hot belt extends well into the temperate belt, and the same range applied to a "temperate" species may extend it far into the hot or well into the cold zone. And it is obvious that a range of more than 6000 feet implies that the respective species is found in all three zones unless it be one of the few species which extend very far up on high mountains.

Species with a range of 4000 feet or less are here called short-ranged; those with a range of 5000 feet and more are long-ranged. Although this is quite an arbitrary distinction the arrangement gives some valuable results.



Of such short-ranged species we have about 55, some of which doubtful as to category.

35 species occur in the Hot-lands, approaching sealevel, and of them 15 are restricted to the Hotlands while 20 ascend beyond them, up to 4000 feet. Nearly all these 35 are native tropical species.

Diagram No. II.

Showing the amplitude of range of 97 species.

The numbers of Southern species are indicated by white circles.

Sonorans by crosses, Nearctics by black dots.

For instance 13 Southern, 10 Sonoran and 2 Nearctic species, total 25, have a vertical range of 4000 feet. — A range of 9000 feet is attained by 2 Sonoran and 1 Nearctic species.

12 species remain within the temperate zone, and 9 of them are plateau species, while the rest are at home on the western and southern slopes of the plateau.

8 or 9 species belong to the cold zone, natives of the higher plateau or of the high mountains.

Of long-ranged species we can consider 42 species.

Of these 27 occur near sealevel. 10 of these are tropical (11 if *Hylodes rhodopis* is included) and of them

4	ascend	to	5000′
2	„	„	6000
3	„	„	7000
1	„	„	8000
1	„	„	10000

Of the other 16 species which occur near sealevel, nearly all can be shown to have descended into the hot countries from temperate or even from the cool zones.

There are further about 7 species which are centred on the plateau, or in the temperate to cool zone, whence they ascend into the cold regions; of these *Manolepis* alone is a Southern, the others are Northern genera.

The rest of the 42 species are made up of such species which do not approach sealevel within 1000 to 2000 feet, but which on the other hand ascend well. or even far into the cold zone.

As might be expected, they are rather heterogeneous: 3 southern genera are represented by *Hylodes palmatus*, *Hyla eximia* and *Trimorphodon ypsilon*, while 3 other snakes, namely *Coronella*, *Zamenis lineatus* and *Tropidonotus* point to the North, besides 2 species of *Sceloporus*.

Or we may summarise that of the 27 long-ranged species occurring in the Hotlands only 11 have Southern, but 16 Northern affinities. Apparently an unexpected result, but another expression of the fact that Southern forms are mostly short-ranged.

The long-ranged species can therefore be arranged into:

I. Tropical species extending upwards beyond the 3000′ level.

II. Temperate species descending into the Hotlands and ascending into the cold zone.

III. Species which are restricted to the cool or cold zone.

Results, which may prove to be of value, derived form com-

parison of the short- with the long-ranged species are expressed in the following table.

	Long-ranged-species Total 42	Short-ranged species Total 55
Centred within the first 3000'	6 = 14 %	38 = 70 %
Temperate	29 or 31 = 71 %	6 or 9 = 11—16 %
Centred at or above 6000'	7	11
Centred at or above 7000'	5 = 12 %	8 = 14 %

This shows 1) that, considering the probable error of such small numbers, the short- and the long-ranged species contribute about equal proportions to the cold fauna; 2) that very few of the temperate group are short-ranged, exactly the reverse of the behaviour of the tropical groups.

Further,

of 44 "Hot" species 38 are short-ranged and only 6 are long-ranged, or 14 %;

of 13 or 18 "cold" species 8 or 11 are short-ranged whilst 5 or 7 are long-ranged = 39 %;

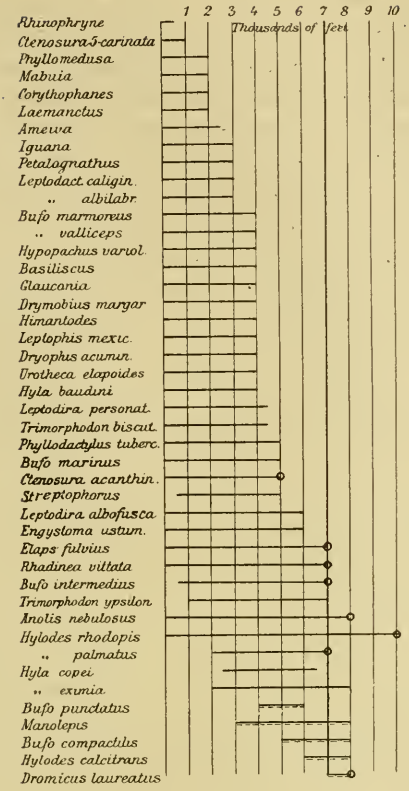
of 35 or 40 "Temperate" species 6 or 9 are short- but 29 or 31 are long-ranged = 80 %.

But if we take all the species promiscuously, which occur in the Hot zone, these amount to about 60, about two-thirds of the whole number available, and in them the long- and the short-ranged species are equally represented! This contradictory result is a strong indication that the dwellers in the tropical Hot-lands are a compound assembly of at least two categories, namely Natives, some of which may ascend ever so far beyond their original hot clime, secondly immigrant descendants from temperate parts, be these the plateau or more Northern regions.

The "Southern" Genera and Species.

(Total 44 species. Diagram No. II, and List A.)

Of these Southerners 35 species occur within the first 1000 feet from sealevel, and thence they extend upwards as follows.



List A.

Showing the vertical distribution or range of 44 Southern species.

Species which attain their unusual toplimit on mountains, are marked with a ring (cf. page 700).
Double lines indicate species modified for exclusively temperate or cold zones.

11	species	remain in the Tierra caliente.	
11	„	ascend another thousand feet to	4000′
5 or 6	„	„	4500 or 5000′
2	„	„	6000
2 or 3	„	„	7000
1	„	„	8000
1	„	„	10000

These 35, out of 42, "starting" from near sealevel, produce in a diagram a regular curve which shows that a considerable number

of species extend from the bona fide Hot-country into the hilly borderland, and then thin out more rapidly beyond.

There are further 8 species which are no longer centred in the Hotlands, not reaching below 2000', but extending their range well into and even beyond the temperate zone. Excepting the monotype *Manolepis* and *Rhadinea laureata* all these partly modified ascendants are Anura: 2 *Hyla*, 2 *Hylodes*, 2 *Bufo*, each of which genera possesses species which indicate a gradual change from hot to temperate and to cold inhabitants; witness *H. baudini*, *H. copei*, and *H. eximia*; or *B. marmoreus*, *B. intermedius*, *B. punctatus* and *B. compactilis*. Further it is most significant that out of the 16 species which at least reach the 6000' level, or which live above it, 8 species reach this high level on solitary mountains, or at least upon mountains or ranges which do not belong to the plateau, where these species are not found; only the two Hylas occur on it. These 8 species seem to have been lured on to the mountains which rise out of the midst of the range of these creatures and have thus invited them to go up to altitudes which sometimes surpass that of the plateau. We may strengthen this interesting fact by including *Anolis nebulosus* which is absent from the Mesa central but to the South of it ascends to 8000'. Moreover of those 8 modified ascendants which themselves, 8 out of 42, amount to 20%, 4 are such mountain-attracted species.

We may perhaps put the result more forcibly by saying that out of the 16 species which at least reach, or go beyond 6000', 8 are modified for higher levels whilst they have given up the Hotlands. Or, if we draw the critical line at 7000', a level which implies a bona fide cool climate, then we have still 12 out of a total of 44, i. e. 29 % which can live there, but half of these (or 6 if we include *Hyla copei*) have changed sufficiently to have given up life in the Hotlands.

Lastly, the Southerners have produced at least 4 species, about 10% of their total, which now live entirely well above the Hotlands: *Hylodes calcitrans*, *Bufo punctatus*, *B. compactilis*, *Rhadinea laureata*; and perhaps *Manolepis* which occurs still on the border level of 3000'. Further, only 6 species have a range of 7000' or more, i. e. 14% only are fit to stand such an amplitude of change as is implied by the difference between the hot and the cold zone. Here it is remarkable that these long-ranged species are still footed near sealevel. This seems so contradictory that the respective species have to be scrutinised. They are:

**Hylodes rhodopis*, up to 10000'
**Anolis nebulosus*, „ „ 8000
**Rhadinea vittata*, „ „ 7000
**Elaps fulvius* „ „ 7000 (?)
Trimorphodon ypsilon, probably going below 1000, and up to 7000'
**Bufo intermedius*, up to 7000.

All those marked * attain this high level on mountains! *Hylodes*, in spite of its enormous amplitude of range, is common, even plentiful, only from 7000' upwards, rare in the Hotlands; *Anolis* is abundant in the tropics, but rare above 7000'; *Rhadinea* is also common in the Tropics, but rare above 6000', and the usual range of *Bufo intermedius* is between 3000 and 5000 feet elevation.

Chief result: Southern or Hotland species ascending into the higher zones are liable to lose their specific characters and to assume others, i. e. they change into different species. Or, if this statement be dislikened: Endemic tropical genera are in the higher zones represented by different, short-ranged species, whilst the long ranged species have attained their long range by having been drawn onto mountains. The latter statement is certainly a sure way of obscuring an important issue. But the fact remains that Southern genera have such species which are now restricted to temperate, or even to cool zones, besides species which are still in the Hotlands although reaching far into the cool; whilst — as we shall see further on — Northern genera possess plenty of species descending right into the Hotlands, or even to sealevel, without losing their hold upon their native cooler zone.

The effect upon the Southerners of ascent or extension into higher altitudes can be traced also in another way: out of a total of 44 species 34 occur in the hot low-lands, within the first 1000 feet, whence their range extends upwards as shown in List A. Let us consider the top levels of these species.

In the following table the second column shows the number of species which actually occur at the various altitudes.

5000'	18 = 41%,	of which no longer at sealevel	9 = 50%	including completely changed species	3 = 33%
6000'	15 = 34	„	9 = 60	„	4 = 44
7000'	12 = 27	„	8 = 66	„	4 = 50
8000'	7 = 16	„	5 — 71	„	4 = 80

Although this mode of calculation gives a surprisingly regular, steady result, it has one weakness. With each new level some species are dropping out whilst others are added, for instance at the 7000′ level *Bufo punctatus* and *Hyla copei* have dropped out from the list of changed species, whilst *Rhadinea laureata* enters as new. Thus it comes to pass that the 6000, 7000 and 8000 ft. levels each possess 4 completely changed species although these are not the same in every case. This unavoidable play of facts may vitiate the statistical result.

Let us therefore make another calculation, taking census for every level of those species only which do not ascend beyond such level, regardless of the fact whether this is their actual upper limit or whether they have already dropped out lower down.

Thus up to 5000′ we have to consider 28 species; of these perhaps only *Streptophorus* does not quite reach sealevel.

Up to 6000′ we have to consider 31 species. Again nothing has happened, excepting that *Bufo punctatus* is introduced as the only entirely temperate species, whilst all the others still proclaim themselves as hot country species, none of them having left the Lowlands.

Up to 7000′ we have to deal with 37 species. A great change is manifest: *Bufo punctatus* as an entirely temperate species; *Hyla copei* almost entirely temperate, nearly leaving the Hotlands. *Hylodes punctatus* in much the same condition; *Bufo intermedius* and *Trimorphodon ypsilon* finding their toplevel at 7000′ and entering the list of those which begin to leave or give up the Hotlands.

This seems indeed instructive. Of the 7 species (if we include *H. copei*) which here at 7000′ have reached their toplevel, only 2 still retain theis footing at sealevel (*Elaps* and *Rhadinea*), all the others having left it. Or to put it more forcibly: being in the act of giving up the Hotlands they thereby are converting themselves into "temperate" species, such as *H. copei* has become almost, *B. punctatus* completely.

Up to 8000′ 43 species have to be considered, nearly the whole total: the Southerners are practically exhausted. Thus far they have been able to ascend at all, besides the hardy, indifferent long-ranged *Hylodes rhodopis*, so that of the 5 species to which 8000′ means actual toplimit, 4 have given up the Hotlands and the fifth, *H. eximia* has given up at least the Atlantic, i. e. the moist, half of the Tierra caliente. Moreover out of these 4 or 5 changed

species only 2 (*H. eximia* and *Manolepis*) can be described as centred in the temperate belt, the remaining 3 having their centre in the cool, *Rhadinea* even well above the temperate zone.

The Northern Genera and Species.

(Total of species 52. Diagram No. III.)

9	species reach, or extend above	12000'	altitude; of these are	5	Sonoran.
11	„	10000	„	5	„
29 or 30	species are found at	8000	„	12	„
30	„	7000	„	13	„ *)
31	„	6000	„	15	„
32	„	5000	„	16	„
36	„	4000	„	20	„
33	„	3000	„	21	„
26	„	1000	„	17	„
22	„	Sealevel	„	14	„

*) Several species find here, or even above, their lower limit.

Most of the species range through several levels and therefore figure repeatedly in the diagram. One half of the Northerners occur at sealevel, more than $^3/_5$ occur within or touch the Hotlands. 9 species, 18%, are centred in the Hotlands, being now restricted to within the first 4000 feet; they have become Hotcountry species, or modified for, or by, the hot climate, against only 9% of Southerners which live completely outside the Hotlands, and against the single Southern form *Rhadinea laureata*, which lives apparently above 7000' elevation, and against 29% of Southerners which reach, or go beyond this level.

13 Northern species, about 29%, have a range of 7000 feet or more, against only 5 Southerners. Or there are about 30% of Northerners which occur within the cold zone and well within the Hotlands, compared with about 20% of Southerners which occur between 3000 and 7000 feet; or only about 16% of Southerners which live well within the Hotlands and also above 7000 feet.

Result. The Northern group contains proportionately twice as many species than the Southerners with so long a range as 9000 feet, and also twice as many species which have been modified for, or by, the

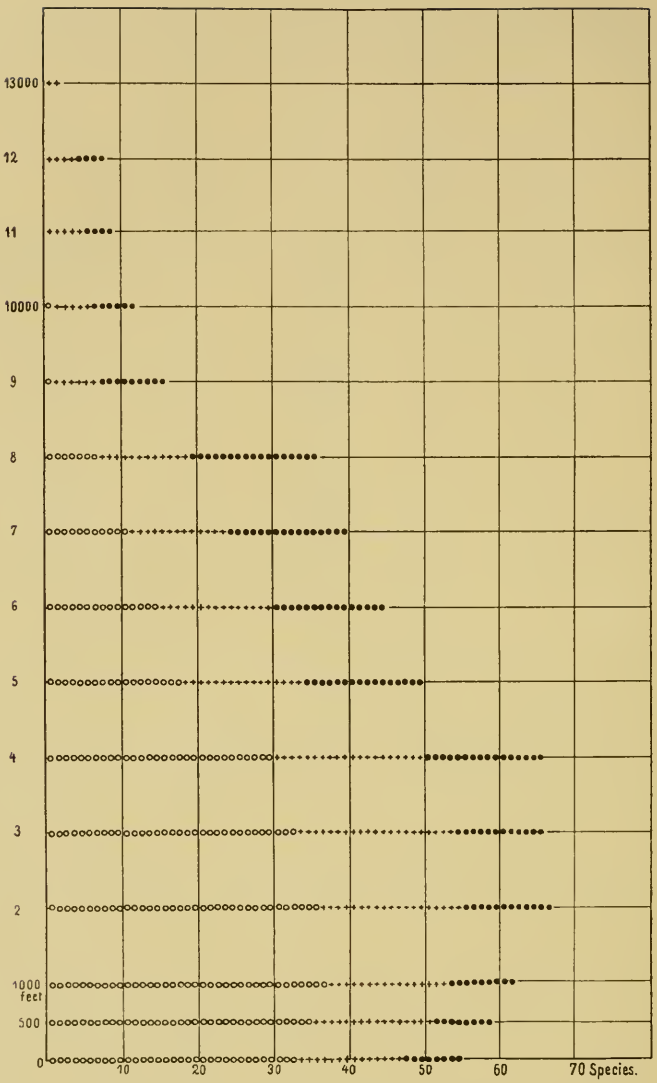


Diagram No. III.

Showing the numbers of Southern, Sonoran and Nearctic species which occur at the altitudes from 0 to 13000 feet.

For instance at the level of 9000 feet occurs 1 Southern, 6 Sonoran and 9 Nearctic species (cf. with Diagram No. I and with Lists A, B, C).

climate different from that of their respective home conditions. Taken as a whole, the Northerners are either hardier (indifferent

to change) or more plastic, i. e. more easily changed by new conditions, than are the Southerners. This seems contradictory!

The principle implied here may easily become a fruitful source of misunderstanding. It has only to be insinuated that accommodation or adaptation implies plasticity. So it does, and yet I may adapt myself to new environment without changing perceptibly, whilst to another person the same shift of environment may mean either death or profound, although healthy change. One has a strong constitution, the other's is plastic, and it is not difficult to guess, which of the two will in the long run be the more successful immigrant. So far as their offspring is concerned, the result is a foregone conclusion. The same considerations apply to our Mexican genera. If a Southern lot of individuals cannot spread into more Northern climes without undergoing constitutional changes, they will in the long run only stock the conquered country with species new to it, but these species themselves being new the original genus is enlarged. But if the Northerners are so strong that they remain what they were, the country's fauna alone is altered by their addition, but not the genus which has merely extended its range. Curiously enough this same drama is now being enacted physically and politico-economically between Mexicans and Americans.

The above calculations would be highly satisfactory if they did not result in the contradictory dilemma that the Northern group is both conservative and progressive. This is a strong indication that this group is not homogeneous, but is composed of two perhaps rather different elements, namely bona fide Northern forms, which for want of a better name are here called Nearctics, and Sonorans. There can be but little doubt that the Sonorans as the aboriginal genera are from the beginning composed of both Hotcountry and Upland forms. Whatever the old Sonoraland, the nucleus of Mexico, was like, it must have comprised coasts, therefore a hot zone although not necessarily low lands, whilst we know that its elevation must have been considerable. But it is only a vague surmise that owing to is long North-South extension its original fauna may have been divisible into Northern and Southern forms. What can we gather about the old Sonoran fauna?

In the list are mentioned 29 Sonorans, out of a total of 52 Northerners.

As Old Sonorans I have treated *Boa*, the *Crotalinae*, *Heloderma*, *Chirotes*, the large genera *Cnemidophorus* and *Sceloporus*, *Phrynosoma*

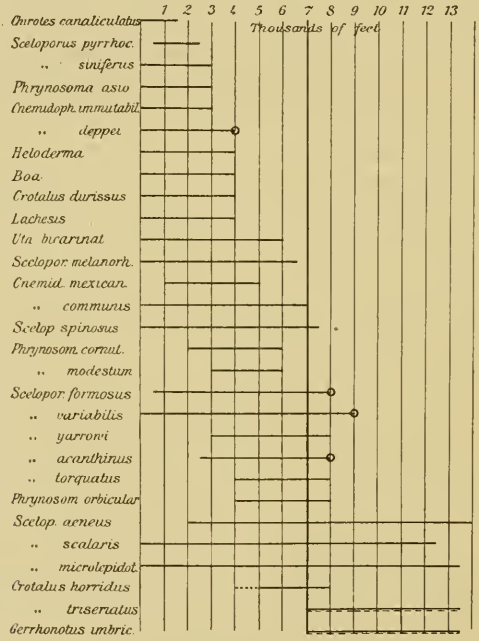
and *Uta* and *Gerrhonotus*. Perhaps *Ctenosura* ought to be added; further *Cinosternum* but not *Chrysemys*.

The "Sonoran" species.

(List B.)

Of the 29 Sonorans 2 species only, *Gerrhonotus imbricatus* and *Crotalus triseriatus* are modified for the cold zone, these alone being restricted to above 7000', at which level occur 14 in all. 17 species extend down to near sealevel, 5% of which are confined entirely to the hot zone and 5 others find their upper level at 4000'. The Sonorans comprise 16 short-ranged and 13 long-ranged species. To the latter belong the 9 species which are entirely or almost confined to the Hot zone, whilst no short-ranged species passes beyond 8000' elevation in marked distinction from the Nearctics.

The Sonorans consequently account for most, about two thirds,



List B.

Showing the vertical distribution or range of Sonoran species.

Species which attain their unusual toplimit on mountains are marked with a ring. The 2 species which have been modified exclusively for the cold zone are indicated by double lines.

of those "Northern" species which occur well within the Tropics and they comprise all those "Northerners" which are confined within the Hotlands or at least within the first 4000 feet. On the other hand they contribute only 2 of the total 7 "Northern" species which are restricted to the cold zone from 7000′ upwards. As about one fourth of the Sonorans have an amplitude of at least 7000 feet, and since they comprise the two species of *Sceloporus* which have the largest altitudinal range on record the Sonorans are certainly accommodating; but they are also rather plastic, having produced species for the hot, temperate and cold zones respectivey. However we must bear in mind that the old Sonoran fauna contained most likely some Hot-country stock and that this may account for the number of tropical forms, so that only those have to be reckoned as "modified" species which are now restricted to the cold zone. To judge from their general distribution and behaviour, the Sonorans are the product of a warm and dry climate, of the Pacific type. As aborigines they must have been longer in the country and therefore had the best chances of adapting themselves to its changes, and two genera, *Cnemidophorus* and *Sceloporus* have indeed become the leading and most characteristic Mexican reptiles.

The mean altitude of the 29 Sonoran species is 4400 feet, against 5700 of the Nearctics. It may seem rather ridiculous to make such calculations, but these results are not at all bad, because they place the average level of the Nearctics at the transitional border between the conventional Tierra templada and Tierra fria, and that of the Sonorans exactly in the middle of the T. templada. The mean for the Southerners is 3000 feet which is rather higher than expected, but as natives of the Hotlands can extend their range far by ascent only, every case of great amplitude must increase the average level whilst a species starting form midlevel may have a much greater amplitude and yet not affect its average level.

It stands to reason that the genera and species of a group, which like the Southerners have all their affinities with Neotropical forms, should, as colonists of Mexico, feel most at home in the Hotlands; and these countries are the first which the immigrants would have to enter in their northward spreading. It is equally reasonable to expect that the Nearctic forms, bred in Northern climes, will find a new congenial home on the higher grounds; that, in fact, they will compensate the loss of latitude by increased altitude, 10° of latitude mean, theoretically, a change of 13,5° F (7,5° C),

equal to a difference in altitude of 4500 feet. Caeteris paribus, and in theory, an elevation of 9000 feet in Southern Mexico has the same mean annual temperature of a lowland country 20° further North, let us say of Missouri.

The division into Southerners and Northerners would be fair enough if the latter were composed of Nearctics only but the Sonorans are the disturbing element. As pointed out before, they are in some respect intermediate, and above all our knowledge is not sufficient to discern in every case between them and Nearctics, although a look at the appended lists shows that these two groups represent two different elements. The old Sonoraland probably continued northwards through California and possibly thence, around the Pacific, was continuous with Eastern Asia. In any case it was and is part of the Pacific division of the Northern hemisphere and it is most likely that the *Amblystomatinae* were some of its oldest inhabitants. That is a question of geological time. On the other hand the Eastern and Northern half of North America is a part of the Atlantic world, more akin to Europe and West Siberia. But since North America became one consolidated entity, the Pacific and Atlantic, or if it be preferred, the Pacific or Western and the Atlantic or Eastern faunas have become mixed, perhaps inextricably.

The „Nearctic" species.

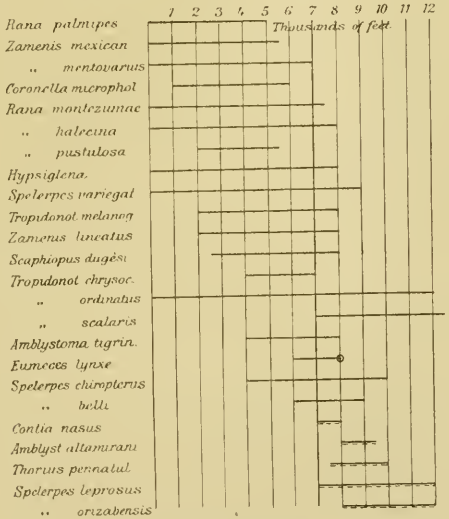
(List C).

There are 24 Nearctic forms, i. e. species the genera of which, we have reason to presume, came into the country from the North, but not from Sonoraland. Of these Nearctics 6 are modified for the cold zone, 5 of them being restricted to levels above 7000 ft. 8 Species extend down to sealevel, two of which (*Rana palmipes* and *Zamenis mexicanus*) have shifted their centre of altitudinal range to a level just within the hot zone, but they have not become exclusively hot country species, as they are still found at the 5000' level. This case is instructive. If we did not feel sure that *Rana* is an originally typical Northern genus, we should declare without hesitation, that a creature like *R. palmipes* was autochthonous of the Hotlands whence it extends upwards well into the temperate zone. In reality it is a member of a Northern genus, but behaves now like a Southern, Central American, species.

The Nearctics comprise 9 short-ranged and 14 long-ranged species.

Of the former 4 are restricted to above 7000' and 2 more are centred at that level, and only one extends down to 2000 feet, whilst none are found at sealevel. But of the 14 long-ranged species one only is restricted to above 7000' and one only is centred up that level, whilst two are centred just within the Hotlands, and 8 in all reach the sealevel.

These Nearctics are further remarkable for the few species which are confined to a strictly temperate range. Most of them being rather long-ranged, naturally extend either into the cold or into the hot zones. The mean of the whole number of specific centres works out at 5700' feet and this agrees well with the mean average altitude which can be deduced from the diagrammatic list of the Nearctics. Most of their short-ranged species belong to the cool or cold zone. That there are so many long-ranged Nearctics, is only another expression of the fact that these Nearctics are more accommodating than plastic. Those which are plastic, have mostly modified for cold life. If we consider the 24 Nearctics and naturalised Mexicans with their average best suitable level of between 5000 and 6000 feet, one third have found their way down to sealevel, although none of these have qualified for exclusively Hotland life; one fourth are modified entirely for the cold zone. Consequently the Nearctics are more influenced



List C.

Showing the vertical distribution of 24 Nearctic species.

by ascent into the cold zone than by descent into the hot lands. This agrees with the chief result drawn from the distribution of the Southerners.

If the main conclusion that change into colder environment, or ascent, is a more powerful factor than descent, allows of general application it would be of far reaching importance. To make sure of this it will have to to tested carefully and without bias by scrutiny of the faunas of various countries. There are no doubt many exceptions which may restrict the conclusion that "temperate" genera produce less easily species which are suited exclusively for hot-country life than species for colder regions. For instance of the two dozen species of *Spelerpes* about 6 seem to be restricted to cold zones, whilst there are perhaps 4 which apparently are found in hot countries only. Of the 21 American species of *Tropidonotus* about 5 seem to be restricted to a warm or hot climate, and a census of the total number of species of this genus, about 70, shows that about half are tropical, many of them being exclusively dwellers in hot countries. Therefore this genus might easily be taken to upset the above conclusion. But it is a genus with an almost cosmopolitan range, and it would be rash to say where it has arisen. It may have originated under typically tropical conditions. However, when we restrict our scrutiny to America, the quest assumes a reasonable aspect. No *Tropidonotus* whatever exists in South America, whilst many of them occur in North America, and very few in Central America. Consequently it is reasonable to assume that so far as Mexico is concerned, these snakes are Northerners which have extended their range southwards.

Why should change from a hot into a cool climate be more easily effected, without harm to the experimenting individual, than the reverse? And why should ascent be more productive of specific change than descent? These two ideas seem to be contradictory.

It is well known that most creatures can endure a temporary change into cooler surroundings, although they may not flourish, while the reverse of such conditions prostrates and often kills them. Amphibia are especially sensitive in this respect; they may be almost frozen, becoming quite lethargic, and they will revive, but a few extra degrees of heat may quickly kill them. Many tropical plants can be cultivated in temperate countries where they have to adapt their oeconomy to shorter summers, whilst Northern plants,

subjected to tropical conditions are mostly failures, since they exhaust themselves through want of rest. Annuals seem naturally to have better chances than perennials.

Temperate Lizards and Tortoises, if not allowed to hibernate, have their lives shortened, because they have lived "too much and too fast", whilst tropical species of the same groups will do very well without such a rest. Of course many creatures aestivate, a condition in many respects resembling that of hibernation, but whilst the latter, if profound, implies almost complete suspension of metabolism and therefore little loss of substance, aestivation often exhausts them much, especially those which pass their torpor in dry surroundings.

Cold can be counteracted in many ways, as by more food, motion, shelter, a more non-conductive coat etc., and if, as with most Amphibia and Reptiles, the temperature sinks nightly or for a whole season, the body simply experiences a rest, to reawaken with the returning warmth. A hot-land species transferred to a temperate country, may find plenty of heat in the day time, even at night without much interruption during a whole season, sufficient for it to lead, so to speak, a three-quarter life each year, and for all we know to the contrary, may thus prolong its entire life reckoned in years.

Not so with a species which is transferred from the poikilothermous temperate to the hot zone with its much more equable climate, which implies always an excess of warmth over what that species was accustomed to. How the physiological process of the self adjusting regulation of the body's temperature works in Reptiles, is unknown, as they neither possess sweatglands nor pant like some mammals. Personally I only know that their mysterious mechanism works most effectively. A snake or a lizard, when caught basking in the sun never feels hotter to the touch than the general temperature, moreoften several degrees lower, but a short time after being left dead in the sun, upon the same spot where it was basking, it becomes disagreably hot. Black tortoises soon become as intolerably hot, through and through, as a block of basalt. This different behaviour of the live and the dead body appears still more striking in our own climate, when, on a hot sunny summer's day the live black tortoise, say a *Cinosternum* never gets overheated side by side with the dead body of another specimen.

Let us apply the general principle, enunciated above, to geo-

logical changes. Elevation of a whole country, or of a range of mountains, or a cold period following upon a warm one would be most productive of new forms; and the same effect should be produced by the spreading of a socalled glacial epoch from the pole. The tropical creatures, coming under the cooling influence will change readily, and the polar species, as the wave passes over them, will be changed into arctic forms, but those which for some reason or other are driven South would remain unchanged, either because they counteract the new climatic influence by their migration, or because, (even if they should spread into hot countries) they can accommodate themselves to their climate, according to the principle mentioned above.

Such a glacial epoch would thus bring about not only a great faunistic intermingling but would actually produce new forms, namely arctics and those transformed Southerners which did not, or could not, withdraw.

What would happen with the turn of the tide, when a warm climate spreads again towards the pole? No changes whatever, except that the arctics will die out or remain occasionally as derelicts, while all the rest, both Northerners and Tropicals alike, will surely reclaim the old ground so far as it suits them; there will be comparatively little making of new species, provided our principle is right that increase of temperature has a minor effect.

Such speculations must not be driven to far. It would be silly to conclude that cold is a more favourable factor to life than warmth, but it is quite a different question whether a change from hot to cold may not have a profoundly stirring influence upon organisms, a case of either change or die. The Permian epoch was one of widely spread coolness and played great havock at least with the marine fauna, by reducing its numbers of individuals and species, but it also ushered in, or prepared, a new and remarkable terrestrial vertebrate fauna. Our last northern glacial epoch may have killed out much of the warm miocene life, but it has given us the present Arctic fauna, which is very considerable and remarkable for being quite up to date, singularly free from oldfashioned types. The place for these are the tropics, because there the climatic conditions have changed least. There are the Hotlands and they have been hot since at least Permian times, and if, for all we know to the contrary, they should have been too hot for typical terrestrial life, then the hot and life sustaining belt would simply have to be shifted away from the equator, to suit our lively imagination.

The vertebrate fauna of the high Mexican mountains comprises no species which are derelicts of an Arctic or Boreal fauna, such as is supposed to exist elsewhere on high mountains within the tropics. The limit of glaciation remained about 20 degrees to the North off the Mexican peaks, a distance like that from London to the Sahara or New York from Cuba. Glaciation absolutely excludes Reptilian and Amphibian life. No doubt there was a cool belt bordering the glaciation of North America, giving the creatures a lead onto the Mexican plateau, or onto and along the Sierras madres which at that time may have had a cooler climate than at the present time.

At an altitude of 10000 feet, on Mexican mountains, the annual mean temperature works out at 11—12° Centigrade (with a January mean of 8° C) like the mean of the coast of California, and taking into account the rather limited fluctuation of summer and winter, and the prevailing moist climate, the Mexican 10000 ft. level resembles much that of the coast between San Francisco to Vancouver. At this level on the Mexican mountains snow is common enough, sometimes lying for weeks, and only during this time reptilian life is suspended in the dominant pineforests mixed with evergreens and some deciduous trees like Oaks, Alder and Arbutus.

Our fauna at and above this level consists of the following.

Hylodes rhodopis
Thorius pennatulus
Spelerpes orizabensis
Spelerpes leprosus
Spelerpes chiropterus
Gerrhonotus imbricatus
Sceloporus microlepidotus
Sceloporus scalaris
Sceloporus aeneus
Tropidonotus scalaris
Tropidonotus ordinatus
Crotalus triseriatus.

Hylodes, as a Southerner, does not count, and we will sink the supposed difference between the five Sonorans and the five Nearctic species. Every one of the five genera has some species living in the United States, but only one of the 10 species occurs also in the States, and this species, *Tropidonotus ordinatus* has such an enormous range, from Canada to Guatemala and from sealevel to 12000 feet, that it is of no value in our question. Further, species which also

occur in the hot zone cannot of course be considered as Arctic „derelicts". Lastly let us enquire into the affinities of the species.

Sceloporus scalaris with *aeneus*, and *S. microlepidotus* each stand rather by themselves in this genus and are moreover typically and exclusively Mexican.

Gerrhonotus imbricatus, and its nearest relations, are confined to Mexico, whilst the widely distributed *G. coeruleus*, Vancouver to Central America does not seem to ascend very high.

Crotalus triseriatus is the high-mountain species of Mexico, whilst on the plateau it is represented by the closely allied *C. polystictus* out of which it seemes to have been developed.

Tropidonotus scalaris is entirely Mexican and the same applies to its closely allied *C. scaliger*.

Spelerpes leprosus, with its ally *S. belli*, and *S. orizabensis* are Mexican only; and so is *S. chiropterus*, but this has its nearest allies in the Eastern and South Eastern parts of the United States.

Thorius, a monotype, is the sole representative in Mexico of the *Desmognathinae*, the original home of which group seems to be the Eastern half of North America. The same seems to apply to *Spelerpes*, but our general conclusion is that whatever has been received by Mexican mountains from the States, be it genus or species, has there been modified into a Mexican species, distinct enough not to be mistaken for a derelict.

In short the inhabitants of the alpine zone of Mexico have been developed there out of other species established at a lower base, unless they have, like *Tropidonotus* simply ascended without undergoing any specific changes.

Nor can it be said that the strictly alpine species of Mexico have developed an arctic or boreal facies, an idea which is scarcely, if at all, applicable to Reptiles and Amphibia, but they have acquired boreal habits, if as such be considered hibernation, endurance of cold and moist ground, and in connexion therewith viviparous habits. It is at least significant that out of the 12 species found at or above the 10000 ft. level all except *Thorius* and *Tropidonotus*, happen to belong to viviparous genera, and that of the genus *Sceloporus* which varies in this respect, *S. scalaris*, *S. aeneus* and *S. microlepidotus* are viviparous.

Cambridge, June 1910.

Lippert & Co. (G. Pätz'sche Buchdr.), Naumburg a. S.