# REMARKS ON THE DISTRIBUTION OF ANIMALS IN SOUTH AFRICA.

BY

JOHN HEWITT, B.A.,

*Director of the Albany Museum, Grahamstown.*

*With 7 Maps.*

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It has long been known that the fauna of the African continent includes a great number of animals which once ranged far and wide in the northern hemisphere. Some of these, such as lions, hyænas, rhinoceros, and hippopotami, lived in western Europe so recently as Pleistocene times, retreating therefrom on the approach of the great ice-sheet. A little earlier, during the latter part of the Tertiary period, the noblest element of the modern African fauna, the antelopes, elephants and giraffes, were all represented both in Europe and Asia: there was even a particular resemblance to our own South African fauna, inasmuch as kudus, springboks, and gazelles, have all been found in Pliocene deposits of those continents. At a much earlier period, in Upper Oligocene times, the bird fauna of Western Europe was akin to that now found in Africa. Secretary birds, ibises, parrots, and trogons, had already made their appearance in France; and the swamps of that country were infested by typical crocodiles.

## PROBABLE SOURCE OF THE AFRICAN MAMMALIAN FAUNA.

It is indeed perfectly clear that most of the present day mammals and birds of Africa are not peculiar to the continent, but are relics of, or perhaps refugees from, the life of the Tertiary period, a life which enjoyed much wider distribution, ranging more or less throughout Europe, Asia, and North America.

There was a time in the history of Africa when the higher vertebrates seemed to have a very promising future. Throughout the Karroo system of rocks, there have been found the fossilised remains of a most prolific and variable reptilian fauna. Amongst those reptiles were forms turning definitely in the direction of mammals, and one of them, *Tritylodon*, is indeed regarded as the earliest known mammal. What became of that fauna we do not know, our knowledge of the terrestrial life of Africa during Mesozoic and Tertiary times being most imperfect. But, with

regard to the ancestry of the present-day mammals of Africa, it may be stated that, except in a few doubtful cases hereafter mentioned, all the positive facts now available suggest their origin, or at any rate their dispersal centre, in the northern hemisphere. In some cases, *e.g.*, the horses and the carnivores, the ancestries have been traced quite definitely in the Tertiary rocks of Europe and North America. In other cases, with less complete ancestry, the past and present distribution is best interpreted in terms of a centre of dispersal in the north, whence they have radiated out in various directions, the earliest types being pushed furthest away from that centre by their more specialised descendants. Thus, antelopes, now most abundant and varied in Africa, seem to have had their centre of dispersal in Asia. Much the same may be said of the giraffes, hippopotamus, pigs, rhinoceros, zebras, jackals, monkeys, anthropoid apes, and lemurs; whilst even man himself, on the distribution data, had his centre of dispersal somewhere about the great plateau of Central Asia.

On these facts, the African continent has been a comparatively passive region. It has merely received successive invasions of refugees from other regions. The earliest invasions of placental mammals, arriving about the beginning of the Tertiary period, and then comparatively undifferentiated, may still have lingering representatives in such forms as the golden-moles and the dassies. There were, without doubt, many forms which have completely disappeared, such as the simplest creodont carnivores and very generalised ungulates, including puny members of a stock which afterwards became the progenitor of elephants. The last invasions included elephants and mastodons, zebras and other single-toed equines, various cats and jackals, baboons and chimpanzees, and a host of modern ungulates. In the long interval between, there had appeared such forms as primitive monkeys and even archaic anthropoids (*Propliopithecus*) as early as Lower Oligocene times, and lemurs probably earlier; then *Anthracotheres*, rhinoceroses and Dinotheriums in Lower Miocene times,[1] and the three-toed horse, *Hipparion*, lived in Northern Africa from an unknown period up to the Pleistocene. Each invasion caused the disappearance of many earlier types through competition, and in this manner Creodonts gave place to true Carnivores, Anthracotheres to hippopotami, and Hipparions to horses: other comparatively simple types like lemurs and okapi, and that primitive ruminant, the water-chevrotain (*Hyæmoschus*), saved themselves by retreating to dense forests, or to limited and peculiar habitats.

This conception of Africa as a mere recipient of animal life, outside the arena of progressive evolution, is based principally on mammalian evidence. The evidence is, however, somewhat deficient, not merely in the imperfection of the fossil record in Africa, but also in the difficulty of correlating in actual time the geological periods of distant regions. As an instance of the latter difficulty, let us glance at a statement made by one authority[2] on the ruminants: "Their representatives in the Oligocene of North

Africa (Fayum) are much more primitive than the contemporary artiodactyls of Europe." Now this is an important part of the evidence that ruminants originated in the north rather than in Africa, but there is certainly an assumption in the statement that the Oligocene periods of Europe and of Fayum were contemporaneous. Various other instances are now known, where predecessors or ancestral forms of modern groups occur as fossils, both in the northern hemisphere and in Africa. In these cases, a northern origin, or a northern centre of dispersal is deduced from the alleged fact that the same form makes its appearance in Africa at a later geological period than in the northern hemisphere; or, comparing the forms of the same geological period in the two regions, those of the north are relatively more advanced in structure. The facts of present-day distribution certainly seem to be in general accordance with this principle, for, broadly speaking, the present day mammalian fauna of Africa is like that of Eurasia towards the end of the Tertiary period; and, further, it is also claimed that the existing mammalian fauna of the Holarctic region includes practically all the last products of evolution, each particular form of that region being structurally more specialised than any relatives it may have in the southern hemisphere, as illustrated by the case of the northern Cervidæ and the West African *Hyæmoschus*.

Such is the essence of the argument for the theory of a northern origin of the successive mammalian faunas of Africa: it involves this assumption—that each division of the Tertiary period as now classified by palæontologists is more or less contemporaneous in Europe and Africa: and it derives its chief support from the data of present-day distribution in so far as it can be shewn that the northern forms are more advanced than the southern ones.

Yet, it would be ridiculous to suppose that so large a continent, with varied physiography and climate, can have been utterly unprogressive. We know indeed that several isolated regions in the southern hemisphere, Australia, South America and even Madagascar, have been important centres of mammalian evolution. Thus, making generous allowance for the distracting influence of repeated invasions of virile stocks from the north, one must expect to find some truly autochthonous groups in Africa. Professor Osborn, in his "Age of Mammals," has urged the claims of Africa to be regarded as a great centre of independent evolution, although the only modern terrestrial mammals for which he could find definite evidence of original African ancestory are the elephants and the dassies, fossil forms of which have been found in the early Tertiary deposits of Fayum in Egypt, and of the latter in East Africa also (mid-Tertiary). With regard to these groups, Osborn's conclusion certainly seems probable, yet is not the only possible one: for we may note that none of the earliest stages of dassie phylogeny have yet

been found, and that, although the earliest stages of Proboscidean phylogeny are known only from the Fayum deposits, yet during the middle and latter part of the Tertiary period, the centre of elephant and mastodon dispersal was in Asia. But, whilst we must suspend judgment on this problem until more material is available from the early Tertiaries of Africa and Eurasia, we may, nevertheless, recognise the existence of truly autochthonous African genera and of groups of genera. Various characteristic elements of our fauna, such as the warthogs, the duikers, and the steinbok, are peculiar to Africa, and quite unknown in fossil form elsewhere. There are, moreover, certain very distinctive mammals only known from the Eocene of Fayum, such as *Arsinoitherium*, a large ungainly creature with a pair of massive horns implanted on the snout; there is also *Propliopithecus*, which is held to be directly ancestral to the gibbons and to all the higher anthropoids, including man himself,[3] which venerable form, be it noted, is said to be distinctly higher than the contemporary *Parapithecus* of the Lower Oligocene of Europe. These facts point to the probability of some independent evolution within this continent at various geological periods: although, I fear that we must abandon all claim to priority in the grandest of living faunas and with it the pet theory of our popular writers—that South Africa is the cradle of the human race!

The doctrine of northern origins and northern centres of dispersal has been widely accepted amongst zoologists, and there is a distinct tendency to interpret the distribution of all groups of animals, and perhaps also of plants, in terms of this theory. It is surprising to note how all facts that seem to point to a contrary conclusion are subordinated. Thus, one well-known entomologist,[4] after presenting the data of bumblebee distribution, expressed himself as follows: "If these data were taken by themselves, a very good case could be made out for the idea that the Bombidæ originated in South America." But he rejected such explanation for several reasons, amongst which was placed first in order of importance the following: "Such does not seem to have been the history of groups concerning which we have fossil evidence."

Another authority[5] on Batrachia writes as follows: "All the families of frogs and toads, except the Brachycephalidæ, seem to have originated in the Holarctic regions, or at least in the northern hemisphere, and to have pushed southwards into southern regions." This is not based on any palæontological data, for, as he tells us quite plainly, "the fossil record gives little aid in determining the past history of the Salientia . . . nor does the fossil record suggest early centres of dispersal widely removed from present ranges." On examining the only data actually available, that of present-day distribution, it is perfectly clear that such a conclusion could not have been reached independently, considering the almost complete absence of primitive

Batrachians in South America (only *Pipa*) and their absence from southern Africa (except *Xenopus* and allies). The Discoglossidæ, which according to the same authority, are the oldest living Batrachians, occur in New Zealand, North America, and the Palæarctic region, and the Pelobatidæ, another primitive group, " whose centre of dispersal cannot be determined until the stru ture of more genera has been investigated . . . still, it is safe to assume that their centre was in the palæarctic region " occur in New Guinea, South West Asia, North America, Mexico, and in Europe.

A third case referable to the same principle, according to a recent writer,[6] is that of certain land-mollusca, the family Helicidæ and allies. He approaches the problem as follows: " Professor Pilsbry's classical hypothesis, that there have been five chief periods or waves in the development of Helicidian life separated from each other by enormous intervals of time, is now very generally accepted, and all these groups are here assumed to have primarily emanated from the most active evolutionary centre and successively spread or are spreading over the whole globe; the most ancient groups, which are also the most primitive in structure, having the widest and most discontinuous range, while the more modern groups follow in the order of their evolution; the more modern the group, the more restricted, concentrated and compact the natural range, each group preserving its relative position in regard to its predecessors and successors. The accuracy of the foregoing deductions is supported by the absence of any trace of the latest developed and most advanced group in any regions except those now inhabited by its constituent species . . . whereas fossil representatives of the earlier groups are actually known to exist in the strata of regions far removed from the area they now inhabit." (See Fig. 1.)

I will not presume to express any opinion on the soundness of this statement as a whole. The main points may be essentially correct, but South African zoologists will certainly note with distrust that the South African data have not been faithfully presented, for the Protogona and Haplogona actually have quite different relations to each other, the former being confined to the western districts of the Cape and South West Africa.[7] On the distribution data, the Protogona (Acavidæ) would, therefore, represent the first wave of migration in South Africa. Attention should also be called to a possibly misleading point in the reference to the fossil representatives. I cannot state how much fossil data is actually available, but certainly it can only be of minor value, inasmuch as conchological characters alone are now recognised as untrustworthy guides to affinity, the modern classification resting on the anatomical basis.

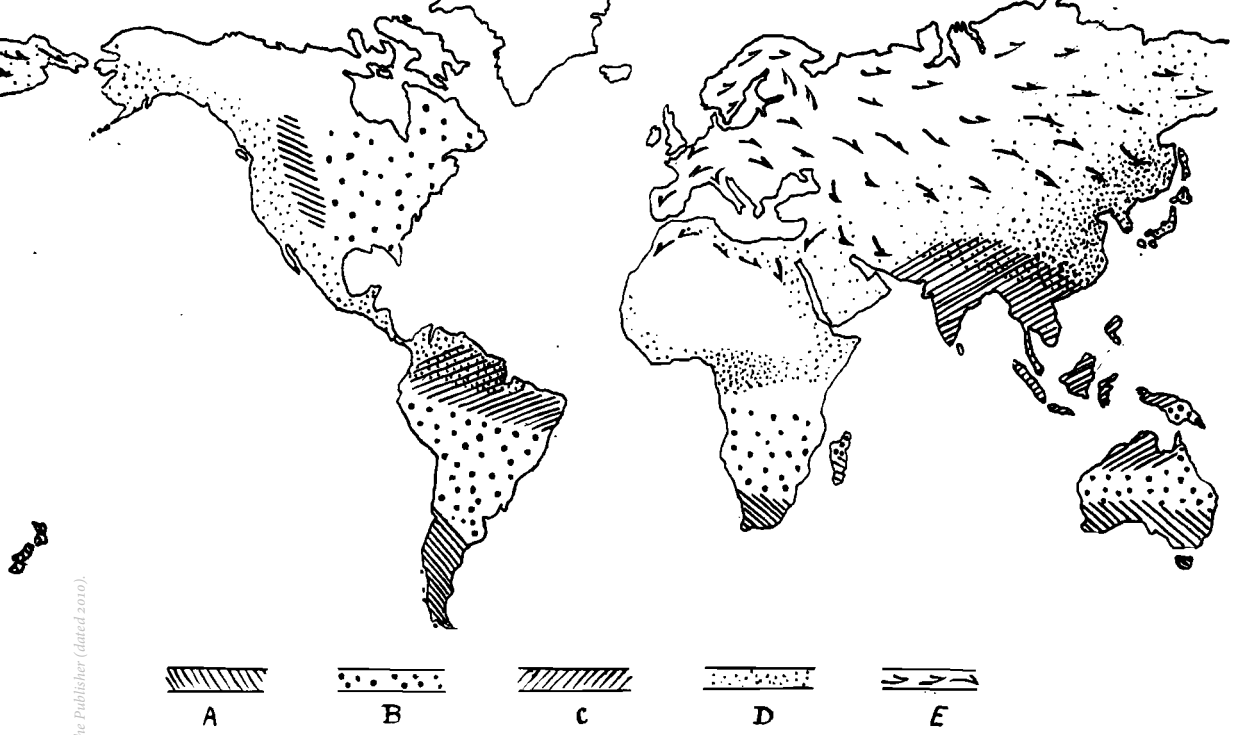


FIG. 1.—WORLD DISTRIBUTION OF THE CHRONOLOGICALLY SUCCESSIVE WAVES OF HELICIDIAN LIFE, according to J. W. Taylor, from *Journal of Conchology*, Vol. XVI, No. 10, October, 1922.

A.—The Haplogona is the most primitive group and the first migratory wave of Helicidian life.

B.—The Protogona constitute the second great wave of Helicidian life, and though dominant over the Haplogona, is largely confined to primitive regions.

C.—The Epiphallogona are the third migratory wave.

D.—The Eudenia are the fourth wave.

E.—The Siphonadenia is the fifth and latest wave and occupies the most active evolutionary area. It is

## A Peculiar Fauna in the Western Province of the Cape.

In the early days of European occupation, all the western parts of South Africa were inhabited by Hottentots and Bushmen. At that time, Bantu-speaking people extended throughout tropical Africa, and as far south as Natal; there were a few stragglers in the eastern districts of the Cape, but they did not penetrate to the region now known as the Western Province. At a more remote period, the yellow races seem to have enjoyed a wide distribution in tropical Africa; but, in course of time, pressed hard by powerful neighbours, they gradually became restricted to the least hospitable parts of the country, the deserts of the west, the sea shore, and the high mountains of the interior.

Now this recent distribution of mankind is paralleled to a considerable degree in the animal world. Thus, amongst lower animals the following instances may be mentioned. A group of large and typical chamæleons occupies all the warmer parts of Africa, southwards to Natal, but is absent from the Cape which is the home of the small species of the *pumilus* group. Similarly, the large hinged-tortoises of the genus *Cinixys*, common throughout tropical Africa, are replaced by small hingeless " padloopers " (*Homopus*) in the Cape. Again, two species of cobras extend far and wide in the warmer parts of Africa, as far south as Natal, but fail to enter the Cape, where, however, occurs a species almost confined to the Cape (*Naia flava*). The common water-frog of the Transvaal (*Rana angolensis*) extends from Angola and Central Africa southwards to Algoa Bay, but is absent from the western districts of the Cape, where its ally *R. fuscigula* is found. Very similar facts are known amongst scorpions and solifuges. The large and characteristic *hostilis* group of *Solpuga* ranges from Southern Rhodesia southwards to the Eastern Cape Province, but has no representatives whatever in the western districts of the Cape, the home of a related but peculiar group of species. A very similar distribution is exhibited amongst scorpions of the genus *Opisthophthalmus*, the *glabrifrons* group occupying the same area as *Solpuga hostilis* and allies.

Yet all this is what some biologists might have predicted, at least amongst groups which have inferior means of distribution; for, a highly distinctive character is given to the western districts of South Africa, inasmuch as they include one large region well marked off from all others in this subcontinent through its prevailing aridity, and another region in the coastal belt is equally characterised as an area of winter rains. But let us note particularly that freshwater animals (water-frogs and fishes) are affected just in the same way as the terrestrial fauna; which facts are not easily explained on appeal to environmental influences as a prime factor.

## Many Primitive Forms in the Western Cape Province.

By far the most noteworthy fact that emerges from our distribution studies is the great number of apparently primitive forms in the Cape fauna, especially that of the west. It is so in all the cases I have just mentioned. The small Cape chamæleons are much simpler than their tropical allies in the characters of the skull and of the lungs; the Cape cobra is simpler than its tropical congeners in the characteristic scaling of the neck; and is also inferior in bodily size; our little "padloopers" (*Homopus*) are like the tropical *Cinixys*, but have no carapace hinge.

Some striking instances of this fact occur amongst the scorpions. *Uroplectes*, our commonest genus of the family Buthidae, includes the small scorpions with stout tail and slender nippers that dwell under stones or in decaying bark of trees. This genus occurs throughout the subcontinent, and has many species, each of which is restricted to some particular area; there is, moreover, very little overlapping of those areas, at any rate in so far as closely related species are concerned. Now, the most primitive of its several groups of species is a western one. Further, whether we consider the genus as a whole, or its individual groups, or the several forms of particular species, in every case we find the most primitive members in the south. The most primitive species of all is *U. variegatus*, known only from the neighbourhood of Capetown. Its more specialised ally, *U. carinatus*, extends from the neighbourhood of Tulbagh as far north as Pretoria and Great Namaland. Of this latter, five varieties are known, the simplest of which is that found at Tulbagh, and the northern forms are most specialised; beyond it, in South Rhodesia, is an allied species, *U planimanus*, which is still more specialised. Again, one group of species, including *formosus* and allies, is limited to the regions bordering the south and east coasts from Capetown to Delagoa Bay; the most primitive member of this group is undoubtedly *insignis* from Table Mountain, and the most specialised species at present known are those of Zululand. Lastly, *U. triangulifer*, a very common species in the central districts of South Africa, has a Cape form definitely more primitive than those of the Transvaal and Natal. (See Fig. 2.)

These facts can only be interpreted in one way. The evidence is irresistibly in favour of successive invasions of types in morphological sequence, differentiated in northern centres, and travelling southwards along three distinct migration routes. These routes are more or less comparable to those followed by the native tribes of South Africa, the eastern route being that of the kafirs, and the western one Hottentot.

No Lamarckian hypothesis of differentiation in situ from some widespread homogeneous stock can adequately explain such a case. Nor may we suppose that radiation northwards from a centre in the extreme south is a satisfactory alternative: for the family has no specialised forms in the Cape as should be the case at a centre of dispersal, and its distribution as a whole indicates the general trend of migration from tropical to South Africa.

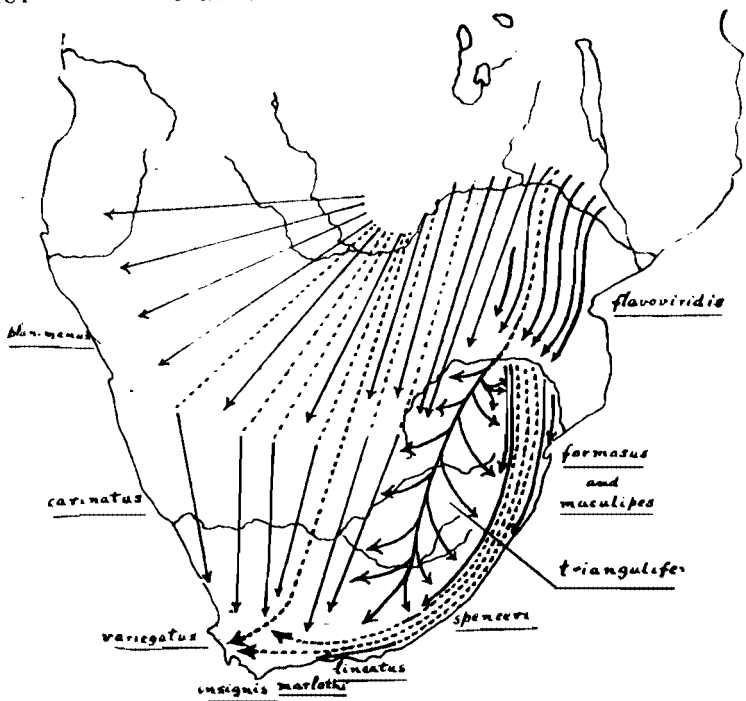


FIG. 2.—DISTRIBUTION AND SUPPOSED LINES OF MIGRATION OF THE SOUTH AFRICAN SPECIES OF UROPLECTES (excluding the xanthogrammus section of East Africa, which is a specialised one). The most primitive species are in the extreme south. [The Mozambique fauna is not well known: probably other species of the formosus group occur there.]

## DISTRIBUTION OF SOME OTHER PRIMITIVE FORMS.

Of course, the most primitive forms are not invariably located in the south-west corner of the Cape Province. The end of a migration route is, however, generally found in some part of the coastal region. A few examples only can be mentioned.

1. The trap-door spiders of the family Migidæ have two genera in South Africa. One of them, *Moggridgea*, ranges throughout southern Africa and has a great many species: terricolous, rupicolous and arboreal. The other, *Pæcilomigas*, with one species only, is confined to the coastal belt of the Cape and Natal, living on trees. *Moggridgea* is decidedly more advanced in structure even when its lowest species are compared with *Pæcilomigas*.

2. Lizards of the family Lacertidæ have their most primitive member, *Tropidosaura*, in the coastal mountains of the Cape Province. I should add that a distinguished authority was inclined to regard another South African genus, *Nucras*,[8] as, on the whole, the most primitive genus of the Lacertidæ; but I am satisfied that

in the uniform scaling of the body and tail, and on the absence of a "collar," *Tropidosaura* is actually the most primitive Lacertid of Africa.

3. The next case presents an element of uncertainty, inasmuch as the coastal forms may be degraded as well as primitive. Lizards of the family Scincidæ are very numerous in Africa.

The dominant genus is *Mabuia*, which occurs abundantly everywhere, and there are many species, both here and in Asia. Some species are sufficiently enterprising to take up their quarters in the midst of towns. In the Cape Province there are five other genera, in all of which the scaling of the head is much simpler than in *Mabuia*. Now these genera are chiefly located in the coastal strip, several being quite unknown elsewhere, and all are rarities except *Acontias*, a genus which occurs also in Ceylon. (See Fig. 3.) Moreover, they are all more or less serpentiform, having the limbs very weak or even absent altogether.

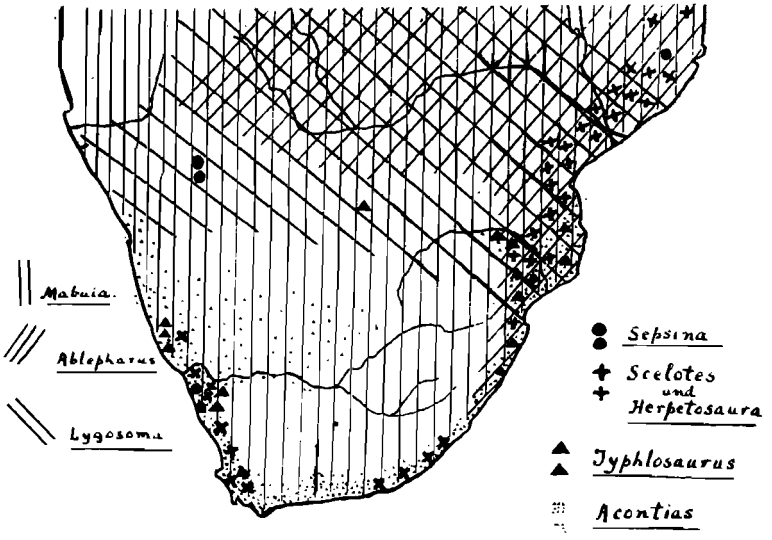


FIG. 3.—DISTRIBUTION OF GENERA OF SCINCIDAE IN SOUTH AFRICA.

The dominant genera, represented by lines, are widespread in tropical Africa, and one of them, *Mabuia*, ranges throughout the sub-continent. The other genera, all more or less serpentiform, are mainly coastal: two of them, *Scelotes* and *Sepsina* occur also in East Africa. *Typhlosaurus* and *Acontias* are active burrowers, and thus may not be in serious competition with ordinary lizards.

Further, two other families of South African lizards, the Zonuridæ and the Gerrhosauridæ, have more or less serpentiform genera, apparently primitive, mainly located in the coastal belt. The best known of these serpentiform lizards is *Chamæsaura*, a genus obviously much simpler in its scaling than the dominant

genus (*Zonurus*) of its family, which occurs throughout Southern Africa. As suggested by the occurrence of *Acontias*, both here and in Ceylon, it may be that some, or even all, of our serpentiform types entered South Africa as such, but the possibility of retrogression in this subcontinent has also to be considered. We may note that in sandy country limbs are sometimes a hindrance to elongated reptiles, and retrogression may thus be a means of their salvation, enabling them to remove from the fierce competition of higher types. Several of our serpentiform lizards (*e.g.*, *Chamæsaura*) certainly have a more extensive distribution than one would expect of a hard pressed inferior stock. But, on the other hand, their distribution does not seem explicable on the assumption that they have been specially adapted to the particular environment they now occupy; for it is difficult to believe that places environmentally so different as Little Namaqualand and Zululand can have a favourable common factor which is not shared also by some of the interior districts.

Again, there is nothing to indicate that our limbless skinks are simply degraded members of the same stock as includes *Mabuia* and *Lygosoma*, the dominant genera, for they seem well separated on external characters. In the distribution of *Mabuia* itself we certainly see an illustration of the general fact that primitive forms are located in the periphery of the continent; the species *M. homalocephala*, of the Cape coastal region, being one of the most primitive of the genus; and *M. trivittata* confined to our region south of the Limpopo being decidedly more primitive than the widespread *M. striata*, which extends throughout tropical East and South Africa, and frequents outbuildings in Pretoria to the exclusion of *trivittata*, which is the common house-lizard at Grahamstown. Thus, we may reasonably believe that early stocks of lizards, whose descendants remain as the various serpentiform genera were pushed to the coastal belt by the recent lizards which now dominate Southern Africa, such as *Mabuia*, *Zonurus*, and *Agama*, all comparatively stout-bodied and strong-limbed.

More rarely, primitive forms have their last place of refuge on the inland mountains, like the last of the Bushmen. For instance, the scorpions of the family Ischnuridæ, which occur throughout tropical and South Africa, also in India and South America, have their most primitive genus, *Cheloctonus*, in the mountains of the Drakensberg system. Its more specialised ally, *Opisthacanthus*, extends along the coastal region from Capetown northwards to the tropics, and is common on the high plateau of Basutoland and the Free State. Here, I may add, that the primitiveness of *Cheloctonus* is inferred from the fact that *Opisthacanthus* passes through a cheloctonus stage in very young specimens.

A comparable case is presented by the species of the lizard genus *Chamæsaura* which extends throughout the coastal regions of the Cape and northwards in the eastern portions of the continent as far as Uganda. Now, without doubt, the most primi-

tive species is *C. ænea*, which occurs over the Drakensberg region, from the Zoutpansberg in the north to the Elliot district in the south. The other South African species are much more specialised and one or other is comparatively common in the coastal districts.

Again, a somewhat unexpected retreat for one of the most primitive of African Elapid snakes is Lake Tanganyika. There, the genus *Boulengerina* lives largely in the water as a fish feeder, a relict type, surrounded on all sides by more specialised forms like the cobras. The same genus has other representatives in the Congo and Cameroons.

Lastly, without entering into details, I may add that various widespread groups of African animals have their most primitive forms not in the extreme south, but in the forest regions of the west coast (cf. map of cobra distribution).

### Widespread Genera Usually most Advanced Morphologically and therefore most Recent..

We have already noticed that, in various instances, primitive genera have a comparatively limited range of distribution. Now the question arises whether all widespread genera are morphologically higher than their associated allies of very limited distribution. Generally, when the contrast in range is great, this must be answered quite definitely in the affirmative. The fact is well illustrated in the lizards of the family Lacertidæ, all the peculiar South African genera being more generalised than *Eremias* or *Scapteira*, which occur also in the Palæarctic region. But, the dominant genus is not necessarily that one which has advanced furthest along the original main line of progress. For instance, the proteroglyphous snakes include a large series of forms ranging from those primitive ones which have many maxillary teeth to the highest which have merely a poison fang in each maxilla. Now, the dominant proteroglyphous genus in Africa is undoubtedly *Naia*, including the true cobras; yet this genus still retains one or two simple teeth in the maxilla, in addition to the poison fang, although the ringhals (*Sepedon*), confined to South Africa, has lost all such simple teeth. The main character in which cobras differ from all their allies is the greater elongation of body and tail; this confers on them the increased speed wherein may be the secret of their success, a character which is specially developed in another dominant genus, the mamba (*Dendraspis*).

Again, the dominant genus amongst South African geckoes is *Pachydactylus*. Like other widespread genera, its fingers and toes are modified as adhesive organs, enabling their possessor to cling firmly in any position to rock surfaces, a modification which is obviously secondary.

Now, in the Kalahari and Namaqualand are other genera, like *Ptenopus* and *Chondrodactylus*, without such adhesive organs on the digits; these are confined to limited habitats, being burrowers in sandy regions.

Apparently, dominance may depend merely on the acquisition of some new character which specially befits its possessor for life in a major environment; yet generally, the dominant stock is the highest type along the main line of progress (Cp. *Eremias*, *Mabuia*, and *Chamæleo* sens. strict.). In the vast majority of cases, there is, unfortunately, no data whatsoever for estimating the period of origin of the various elements of our fauna, nor the time of their arrival in South Africa.

We must assume that specialised genera are more recent than their more generalised allies, despite the wider distribution of the former. Admitting a genetic relationship, no other conclusion seems possible, unless the apparently generalised forms are really degradation products from the dominant stocks. Now the independent testimony of palæontology and of embryology gives us confidence in the belief that the evolution process is not strictly reversible. For instance, when certain mammals acquired marine habits they still remained essentially mammalian in structure; their gill slits did not reassume the original piscine form and function, and in short the morphological changes that accompanied the change of habit were not reversions but specialisations. The principle is sometimes referred to as the Law of Irreversibility of Evolution. Degradation processes do actually occur in many groups of animals, but the products are peculiar rather than generalised forms. Therefore, we are well justified in regarding generalised forms as merely relict members of the original stock from which more specialised ones have arisen.

I am aware that an eminent botanist[9] has put forth the view that the dominant genera of plants are all old ones, and the genera of limited range comparatively recent. This, if applied to the groups of animals now under consideration, must mean that our generalised genera are indeed degradation products. A decisive solution of the question of their status may not be obtained without the aid of embryological data. Only in one case (*Lophosaura*, the Cape chamæleon) amongst our endemic reptiles is there any such data at present; which, I may add, does not in the least suggest that *Lophosaura* is merely a degraded product from the typical chamæleon stock.

In any case, I would not suggest to you that all widespread genera are recent in origin. There are, for example, two widespread genera of burrowing snakes—namely, *Typhlops* and *Glauconia*, the former ranging throughout the warmer parts of the world, and the latter throughout South America and Africa. These are primitive snakes with no known allies, and may have persisted unchanged for very long periods in the absence of competition from nearly related higher types. Such instances are not very common, and, actually, the great majority of widespread genera are morphologically the highest members of well-established groups, and thus relatively recent.

## Struggle for Existence Most Severe between Closely Related Forms.

The general rule that a recent specialised genus tends to monopolise the land, driving its more generalised predecessors to the periphery of the continent or to unfavourable environments, is worthy of acceptance. But there are limits to the operation of this rule. Sometimes, primitive and specialised forms co-exist, apparently without mortal competition, in quite limited areas. One striking instance is afforded by the snakes of Africa. There are five families, none of which are peculiar to Africa; these represent various grades of evolution and may have entered the continent at different periods, yet representatives of each may be found in all warmer parts of the continent. In one of these families, the Colubridæ—which includes all typical snakes, except pythons and adders—primitive and specialised forms occur side by side in every part of the continent; the poisonous Proteroglypha, which have certainly passed through an aglyphous non-poisonous stage, have nowhere monopolised the land to the exclusion of Aglypha. Along with these Colubridæ, there occur almost everywhere the Glauconias, those worm-like snakes, which, if we may judge by their comparatively well-developed pelvic girdles, are the most primitive of all snakes.

Nevertheless, there is abundant evidence of the operation of the rule amongst snakes, but only within groups of closely-related forms. Such a group is that of the cobras and their allies, the ringhals (*Sepedon*), and the shield-snouted snakes (*Aspidelaps*). The cobras occur throughout Africa and Asia, being dominant amongst poisonous snakes. They have specialised in the direction of speed and of size, the genus *Naia* including that veritable giant amongst Colubridæ, the Hamadryad of Malaya, which is said to reach a length of about 15 feet. Now, the nearest allies of *Naia* are two South African genera, *Sepedon* and *Aspidelaps:* these are severely limited in distribution and are definitely inferior to *Naia* in speed and in size.

Further, we may note that, although cobra and ringhals may occur in the same districts, they are not found in close association; near Grahamstown, the ringhals, along with berg-adders and other inferior reptiles, is confined to the sour-veld mountains, whilst cobras occupy the warmer sweet-veld. On these facts, we are entitled to explain the restricted distribution of the two inferior genera mainly as a consequence of competition with *Naia*. Moreover, the result of a detailed analysis of the distribution of the various species of *Naia* within the continent of Africa inspires us with confidence in that conclusion, for it is perfectly clear that the highest species of *Naia* such as *N. nigricollis*, are the most widespread (see Fig 7), whilst the more primitive species are greatly limited in distribution, the yellow cobra of the Cape being one of the latter. From all these data, we may therefore infer that competition is most severe between forms which are very closely related, and becomes practically non-existent between groups of remote relationship.

## Centres of Specialisation in a few Old-world Groups of Reptiles and Arachnids.

We are now in a position to consider a few facts of distribution which seem relevant to the problem of the origin of our fauna. Let us admit at once that, in the absence of palæontological data, we can never hope to ascertain where the main groups originated. But, we can at least trace the migration routes of many groups with considerable degree of probability and the region of recent specialisation can be recognised.

In those groups which have been derived from the northern hemisphere, we must expect to find the various forms arranged in regular morphological sequence along the routes of migration; the highest types should be located in the north, some of them perhaps still in the Palæarctic region, and the lowest types should be in the extreme south or west of Africa. On the other hand, if any groups have evolved in Africa, we must expect to find the highest types within this continent, and the lowest ones dispelled in all directions, some in the Palæarctic region, and others perhaps in South or West Africa.

Now, on careful analysis we actually find some groups of animals have their most specialised forms in Africa, and more generalised ones in the Palæarctic region; usually, however, the most specialised forms of the Old World are located partly in Africa and partly in the Oriental region; in various instances, there is a subsidiary or even a principal area of specialisation south of the Zambesi. These conclusions are based on such data as the following, presented as concisely as possible:—

A.—Solifugæ occur in the warmer parts of the Old and New Worlds. The primitive genera have single-jointed tarsi, and the most specialised genera have the hind tarsi 7-jointed. The latter constitute the sub-family Solpuginæ, a group confined to Africa, but surpassing all others in its distribution throughout the continent and in the number of its species. (See Fig. 4.) South of the Zambesi, this sub-family has evolved a group of species characterised by gay colours and sun-loving habits, which is noteworthy, inasmuch as Solifuges generally are nocturnal animals and sombre coloured; these diurnal species are, moreover, highly specialised in the flagellum and dentition of the males. Now the related, but far simpler group, Rhagodinæ, also enjoys a wide distribution, extending through Asia as far east as Cochin China; but in Africa does not range south of the Equator. The Galeodidæ have a somewhat similar distribution, and these also are simpler than the Solpuginæ, in several respects.

Again, the dominant and most specialised genus of the sub-family Dæsiinæ is *Dæsia*, which extends practically throughout Africa, and as far as Arabia and Palestine. Now, all the related genera at the fringe of its range are simpler in structure; such are *Gluvia* of Spain, *Gluviopsis* extending from the Eastern

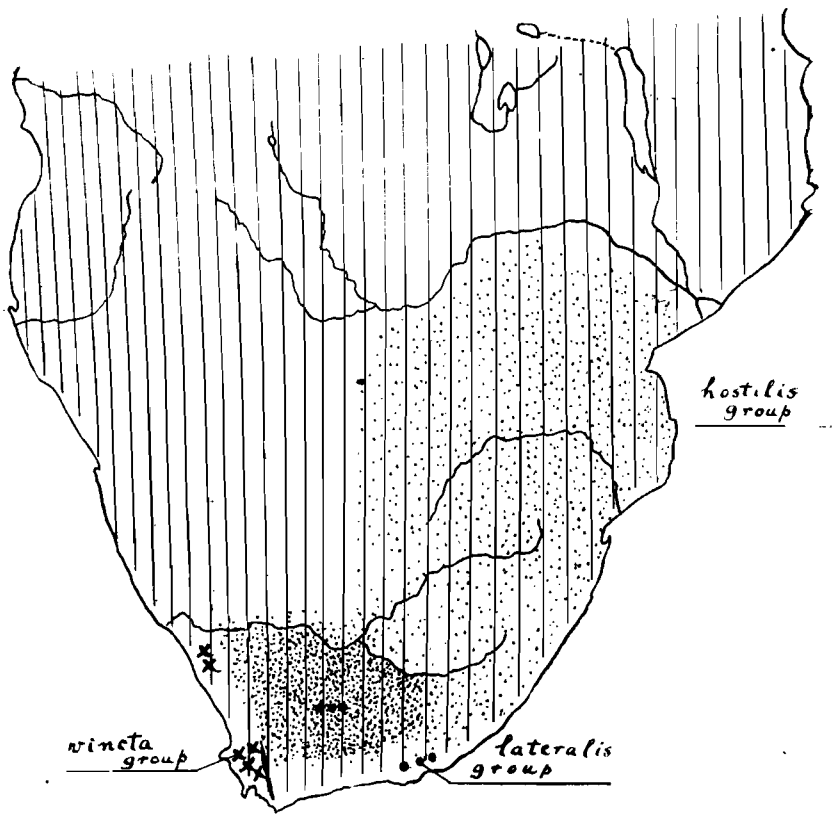


FIG. 4.—DISTRIBUTION OF SOUTH AFRICAN GROUPS OF SOLPUGA (excluding those of Namaqualand).

Primitive nocturnal species, represented by lines, occur throughout. The others represented here are all diurnal and are the most advanced of the genus. The hostilis group, widespread in the eastern half of the sub-continent, is replaced by the related chelicornis group in the Karrooid regions of the Cape. The vincta group is more primitive in dentition than the species of the high plateau, and the southern members of the hostilis group, such as derbiana of Grahamstown, are also somewhat more primitive than the northern ones.

Mediterranean region to Western India, and *Gnosippus* of Egypt and Palestine. Within Africa are also a few generalised genera, amongst the simplest of which is *Melanoblossia*, which has a very narrow range in the western Cape Province.

It seems permissible to interpret these facts as follows:—There has been without doubt a centre of evolution in the African continent, especially in the south, where the drier conditions favoured the establishment of very specialised species. Some of these acquired diurnal habits and became conspicuous elements of our fauna. As the specialised genera spread, they appear to have pushed out their generalised allies, some of which reached Europe, Asia and America.

B.—Scorpions, of the sub-family Scorpioninæ, range throughout Africa and Asia. The group is a very homogeneous one, and it is difficult to trace the former lines of dispersal from the available data. The South African genus *Opisthophthalmus* includes many species, referable to several groups. One of these groups, that of *O. glabrifrons*, is more specialised than any other member of the sub-family, especially so in the posterior position of the eyes. This group occurs only in South Africa, ranging from the Zambesi almost as far as Capetown. (See Fig. 5.) Other groups of the same genus are quite normal amongst Scorpionine genera in the ocular characters, and these groups occur north, west, and south-west of the specialised one. Compared with *O. glabrifrons*, the North African genus *Scorpio*, and the Kalahari species *O. carinatus*, have remained primitive. Thus, just as in the case of the diurnal Solpugas, there is clear evidence of progressive evolution having taken place in Southern Africa.

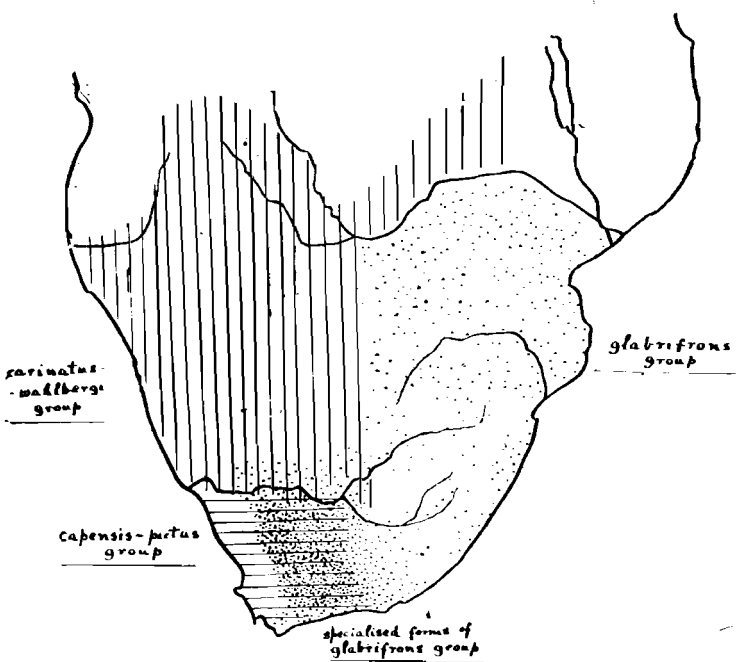


FIG. 5.—DISTRIBUTION OF GROUPS OF THE GENUS OPISTHOPHTHALMUS.

The dotted region is that of the most advanced types. The carinatus-wahlbergi group is most primitive. The capensis-pictus group is also primitive relative to the species in the eastern half of the sub-continent.

C.—Lizards of the genus *Mabuia* have many species in Africa, Madagascar and Asia, and a few in Central and South America, and the West Indies. Now the most specialised group of species is clearly that of *M. striata* and allies, which is confined to Africa, ranging from Abyssinia southwards to the Cape. There are related genera in the northern hemisphere, one of which, *Eumeces*, occurs in North Africa, Asia and North America; but so far as I can see, this genus is not more specialised than *Mabuia*, and, indeed, is more primitive in one respect, the constant presence of pterygoid teeth.

D.—But if there is some doubt whether the northern genera of Scincidæ are higher or lower than *Mabuia*, the true state of affairs seems clear enough in another group of reptiles, the viperine snakes. One authority, Miss Joan Proctor, speaks of *Vipera ursinii* of Central Europe as the " apparently most primitive form amongst living vipers." This conclusion is based on the accepted view that Viperidæ are direct derivatives of Colubridæ. On that view, genera with head-shields still existing are more primitive than those which have numerous small scales on the head, and likewise forms with about 19 rows of body scales are more primitive than those with many such rows. Leaving out of consideration such genera as *Causus* and *Atractaspis*, which are probably not related to the true vipers, the various forms arrange themselves in the following order:—

1. In Europe and Asia the most primitive members (*Vipera*).
2. In Northern Africa and Southern Asia, the most specialised forms (*Echis*, *Cerastes*, etc., and most advanced species of *Vipera*).
3. In tropical Africa moderately specialised forms (*Atheris*, *Bitis gabonica*, *B. nasicornis* and *B. arietans*).
4. In Southern Africa, still less specialised forms (our peculiar species of *Bitis*, such as the berg adder).

These data are interpreted as indicating a centre of dispersal in some part of the region between North Africa and Southern Asia. Thence the primitive forms were radiated out, some to Europe, and others to the extreme south of Africa. (See Fig. 6.)

This case well illustrates what is evidently a general rule amongst reptiles, that the specialised forms are larger than their more generalised relatives. The primitive *Vipera ursinii* is quite a small species, and so are the berg-adders and horned-adders of Southern Africa as compared with the adders of Asia and tropical Africa.

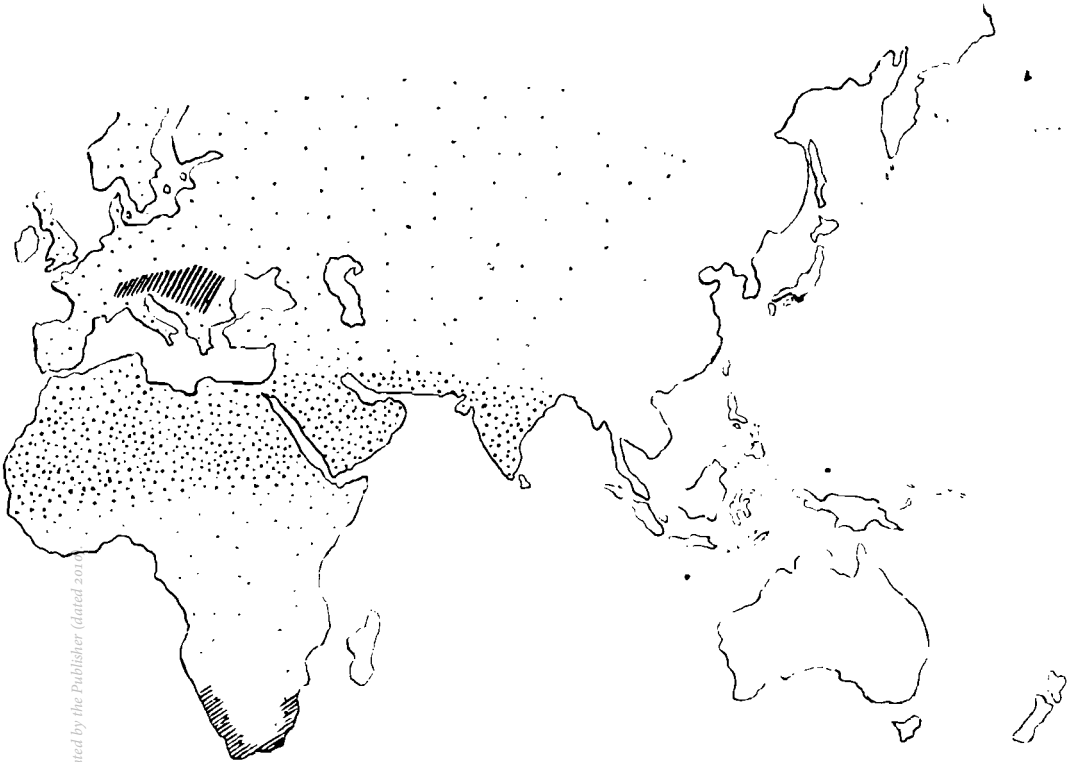

FIG. 6.—DISTRIBUTION OF FAMILY VIPERIDAE.

The densely dotted area is that of the most advanced types, north and south of which is a large area occupied by more primitive types. The oblique shading in South Africa indicates distribution of the primitive species of *Bitis*, that in Central Europe the distribution of *Vipera ursinii*.

E.—There is much probability that cobras (*Naia*) are of African origin. The species are referable to three groups, all of which occur in Africa, but only one has representatives in Asia. Each of the two groups peculiar to Africa has primitive forms located in western portions of the continent and specialised ones of very much wider range. The third section common to Asia and Africa is composed of specialised forms with no very primitive members. Its occurrence in Asia may be a result of direct spreading from Africa (See Fig. 7.) Now, the genus has its nearest allies in two South African genera, and there is another related genus in Egypt, *Walterinnesia*. The location of these related genera in South Africa and Egypt is explained as due to pressure from the overpowering genus *Naia*, centrally produced. The presence of *Walterinnesia* in Egypt seems against the probability of *Naia* having entered Africa from the north.

F.—Three families of lizards are characteristically African. One of them, Zonuridæ, is quite confined to South and East Africa; another, Gerrhosauridæ, is rather more widespread in Africa and has also representatives in Madagascar; a third, Chamæleonidæ, ranges still more widely, occurring throughout Africa and Madagascar and having one or two representatives in the Mediterranean region and India.

Lizards of the genus Zonurus are very sluggish in habit, and more or less rupicolous; so, considering the extensive range of the genus in South and East Africa, it must have been here for a very long period. There is nothing to indicate that its most northern forms are higher than those found in the Cape. *Zonurus tropidosternum* of East Africa is one of the nearest allies of our coastal *Z. cordylus*, and the *cordylus* group is certainly less specialised than the much larger species, *giganteus*, of the Free State, or *cataphractus* of the Western Province, or *macropholis* of Little Namaqualand. Now, on the characters of the scaling, the serpentiform genus *Chamæsaura* should be regarded as the most primitive of the Zonuridæ. Unfortunately, the distribution data of Chamæsaura are not easily interpreted, for the northernmost species, *tenuior* of Uganda, is a specialised one, but not the highest of the genus, whilst the southernmost species *anguina*, is more primitive, but not the lowest of the genus. The most specialised species of the genus is *macrolepis* of Zululand, and the most primitive is *aenea* of the Drakensberg region. Considering the family as a whole, the available evidence suggests that the several forms found north of the Zambesi have been derived from South Africa; and, in any case, even if the group is not entirely southern in origin, it cannot be doubted that most of its specialisation has occurred in this subcontinent.

Chamæleons also present evidence of much specialisation within Africa, especially in the forest regions of the west, and in the island of Madagascar. The fact that the several Mediterranean and Indian species belong to one of the specialised sections of the family need not imply a northern origin, being easily

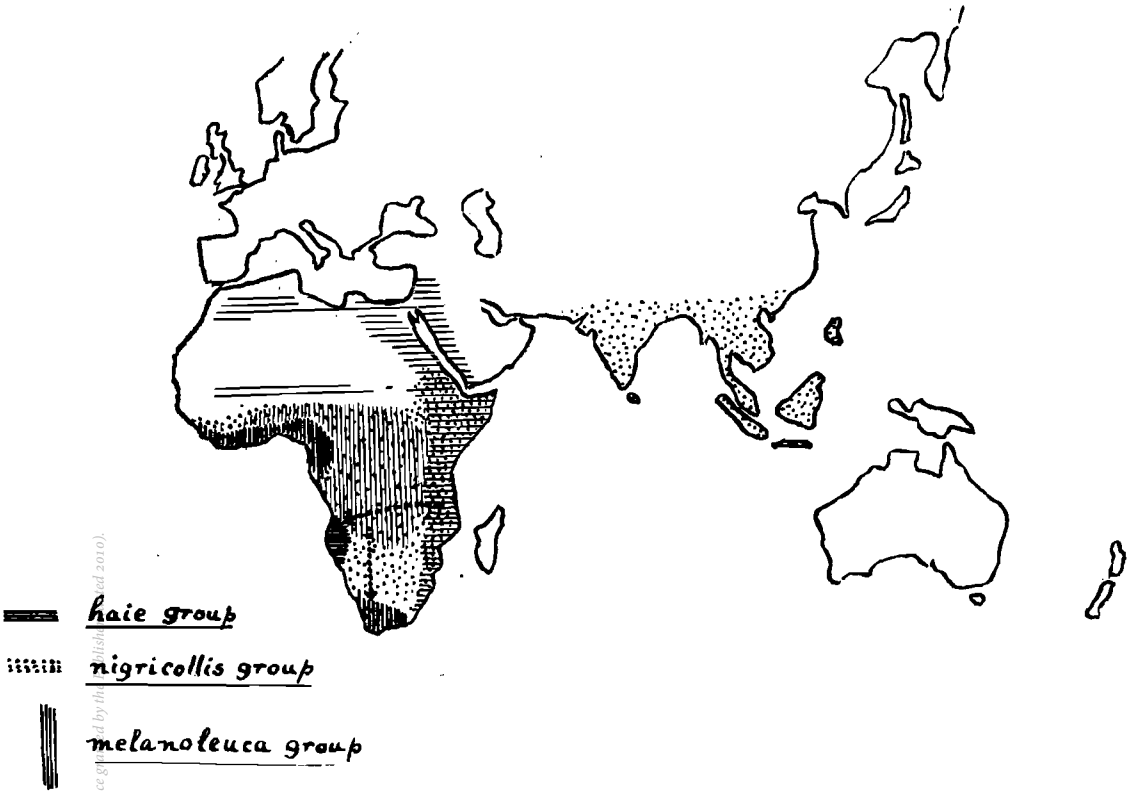


FIG. 7.—DISTRIBUTION OF THE COBRAS (NAIA).

The three thickly shaded areas on the west side of Africa are inhabited by more or less primitive forms belonging to the *haie* and *melanoleuca* group.

explained as the result of migration from tropical Africa. Moreover, if chamæleons had their centre of dispersal in Asia, or in the Palæarctic region, it is difficult to understand their complete disappearance from those regions but for the few species above mentioned; we might expect to find other and more primitive members in the Himalayas or the Malay region, where none whatever occur at present. There are certainly many arboreal lizards in the dense forests of the latter region, such as large green Agamids and geckoes; but, considering the remoteness of their relationship to chamæleons, they should not be regarded as deadly competitors, and, indeed, arboreal forms of all three families occur in Africa. Still, chamæleon remains have been reported from Oligocene deposits in France; the record may be unsatisfactory, for it was ignored by Dr. W. D. Mathew, Palæontologist of the American Museum, who expressed the opinion that chamæleons and Zonuridæ are of Ethiopian evolution.

In the Gerrhosauridæ, the most specialised species of the dominant genus is clearly *Gerrhosaurus validus*, which ranges from the Zoutpansberg district to the Zambesi. This species is the giant of the family. North of it is a homogeneous section of large forms ranging from Togoland and Abyssinia southwards to Zululand. South of it, no centre of specialisation is recognisable in this genus, the common Cape species, *G. flavigularis*, being very similar to the tropical *G. nigrolineatus*, but smaller. In the genus *Tetradactylus*, the most primitive forms are in the south-western Cape Province and Natal; specialised forms of the same genus occur in northern and eastern parts of the Cape Province, in Natal, Zululand, Transvaal and Angola, and another limbless form has been recently recorded from Barotseland. (*Paratetradactylus*).

Whilst we may without hesitation accept the view that the two former families have undergone much specialisation in Africa, it is remarkable that no generalised forms in either case are known from northern Africa, as seems required on the theory of a southern origin; possibly such forms did not survive the general desiccation which is known to have occurred in Northern Africa during Pleistocene times, when extensive faunas of typical African type utterly perished. The Gerrhosauridæ also may be truly autochtonous in Africa. They are intermediate between Lacertidæ and Scincidæ, which are both well developed in Africa.

The data just presented is sufficient to show considerable improbability in the view that the centres of progressive evolution have all been located in the northern hemisphere. The idea that the northern fauna is made up solely of the highest types cannot be maintained. Now, we know that the African continent, unlike Europe, has been stable more or less throughout Tertiary times. and that from Miocene up to Pleistocene times, Africa was closely connected with Europe and Asia. It seems reasonable, therefore, to accept what is undoubtedly the simplest interpretation of the distribution data; that the area of active evolution was not far

removed from the modern specialisation centres, at any rate in well-established old-world groups, which have primitive forms in the north as well as in the south. The specialisation area of each group may have contracted and expanded during changes of climate, but apparently has never advanced northwards to a great extent, seeing that the primitive forms have not reached North America. On this view, a good deal of progressive evolution has occurred within the African continent occasionally in the south sometimes in the equatorial forests, often in the savannah regions of East Africa and perhaps most frequently in the zone of hot country, comprising North Africa, Arabia and India. The two latter regions have been the most important; from them a succession of primitive forms has been dispersed in all directions. We may suppose that the southern waves of dispersal have in great part survived, whilst many of the northern ones perished during the great climatic changes of the Pleistocene period. In a few other cases, these primitive forms found their way to South America, apparently by a direct route. In the Solifugæ, for example, the fauna of South and Central America is closely allied to the primitive Dæsiine genera of Africa, whilst that of North America is in some respects still more primitive, and altogether different from the Palæarctic Solifuge fauna.

### Geographical Forms and Subspecies.

Besides the Linnæan species, we have to recognise the existence of a vast number of geographical varieties and of local forms. Can we explain all these various forms as mutually conflicting varieties driven through mortal competition to the parts they now occupy; or, are they purely of local origin, each form arising within its own area from an original common stock?

Now, in South Africa, the distribution of the various geographical forms of a species is in some cases correlated with floral regions sufficiently closely to justify the conclusion that environmental differences have directly or indirectly contributed to the diversity of form; it would be reasonable to suppose that had the environment been a uniform one, no such diversity could have been perpetuated, even if it had arisen. As an illustration of this, the geometric tortoises may be mentioned; they have one well marked form in the south-west corner of the Cape Province, another extending widely in the Kalahari, also forms in the Karroo, Eastern Cape Province, and in Little Namaqualand. These forms are tolerably distinct, some of them possessing characteristic features of considerable constancy; nevertheless, there is some intergrading between them.

But as often as not, the correlation of distribution with physiographic or climatic changes is very hypothetical. In many cases amongst scorpions, trapdoor-spiders, and other slow-moving creatures, the occurrence of several closely related forms within areas of limited size and apparently uniform conditions makes it difficult to connect differentiation of form with environmental

differences, except on the assumption that no two portions of the same area can possibly be identical in character. Remembering also how considerable is the variation amongst associated members of a species, and even amongst individuals of a litter, we realise that variation must occur even in uniform environments. Some will, therefore, think it unnecessary to assume that changing environments have in any direct manner caused the present diversity; the environmental factors may have operated solely in affording increased facilities for the isolation of mutually antagonistic forms. This is evidently what has happened amongst the races of men. The yellow races of South Africa have been allowed a free hand in the Cape Province for many centuries, probably because the arid conditions of the Cape were not sufficiently attractive to Bantu tribes. Certainly there is no good reason for supposing that the yellow character has been acquired by Bushmen in response to environmental impulses in South Africa; nor that negroid races are black because something in their environment on the Equator, or in dense forests, has made them so; for we know that in other parts of the world, as in Malaya, the human population of equatorial jungles is comparatively pale.

Further, the fact that in many cases subspecies are distributed in regular morphological sequence is not only difficult to explain in terms of environmental influences, but is also evidence against the view that each form is of local origin.

Nor need we suppose that each distinctive character of any one form has some relation to peculiar local requirements, for some of these characters are probably original ones which have travelled great distances. For instance, the spotted ventral surfaces of the African form of the barn-owl may not be a special adaptation to African conditions, but rather a primitive feature once found also in their northern ancestors; this view accords with the fact that immature specimens of many birds are spotted. Similarly, the fact that all our endemic birds of prey are smaller than their respective allies in Europe may merely mean that our small forms are refugees from the north. In like manner we may explain the white-bellied form of the little bush-warbler. *Apalis*; in this genus, all the forms ranging from the Eastern Cape Province to East Africa, are yellow-bellied, but that in the Western Cape (*A. claudei*) has a white abdomen.

It would be rash, however, to assert that environmental influences can never directly operate in the formation of geographical forms, for the possibility of local evolution must not be excluded. According to Mr. A. Roberts,[10] our South African birds of prey, though smaller than their European representatives, are, nevertheless, larger than those of equatorial Africa; he expresses this as a general rule—"species found in the tropics are nearly always smaller than their allies found towards the poles."

Does this indicate a secondary evolution of large forms in South Africa; or, is it possibly a result of original segregation, the

environment exerting nothing more than a guiding influence in the arrangement of the various forms? The former view seems preferable, if the whole tropical belt is occupied only by small forms as appears to be the case.

Evidence of local evolution may also be found in certain adaptation characters. Amongst some of our lizards there is a peculiar modification in the characters of the lower eyelid. This, in certain species, is quite transparent, enabling the creature to see with eyelids closed, which is generally held to be an adaptation to conditions of windswept deserts. The transparent lower eyelid occurs in genera belonging to several distinct families. In some cases (*Ablepharus*), the character is generic and was almost certainly evolved in the north, for only one of its many species has reached South Africa. In other cases,. such as *Ereurias pulchella*, the evidence points to a certain amount of evolution in South Africa, for the character reaches its maximum development in several South African species, although the genus is apparently of northern origin and some of the North African species also have a more or less transparent eyelid disc, formed usually of two scales, frequently of several, seldom of one scale. Actually, all the South African species—except *lugubris*, which occurs also in Angola and Southern Rhodesia—have lower eyelids either transparent or more or less semitransparent; those of East Africa, including *lugubris*, have opaque eyelids; those of North Africa again, have more or less semitransparent eyelids; and, lastly, those of Central Asia have opaque eyelids. There is thus an indication that the character actually originated independently in North and South Africa. According to some systematists, the specific differentiation of our fauna is mainly of local evolution, even though the genera arrived as such from other regions. Thus, when dealing with the distribution of the Agamid[11] and Lacertid lizards, Mr. Boulenger represented both these families as of northern origin with unmodified ancestral forms still in tropical Africa, and the most specialised ones in the extreme south. He regarded the northernmost species, *Nucras emini* of Lake Victoria, as the most primitive of its genus, and similarly *Agama mossambicus* of Nyassaland, Northern Rhodesia and Portuguese East Africa comes nearest in his view to the prototype of the original Agamid stock of South Africa, whilst typical *Agama hispida* of the south-west Cape is most remote from the hypothetical ancestral form. Apparently, a single invasion from the north was assumed; in the north there remained portions of the original stock, but the main stock, passing southwards, modified more and more the further it progressed. Now, this arrangement is quite different from that I have represented to you as normal; theoretically, it seems possible, for, as we have seen, secondary centres of evolution have in some cases arisen in this subcontinent. Yet, there may be some error in the premises, for the occurrence of the most specialised forms in the south-west corner of the Cape and more generalised forms radiating therefrom in morphological sequence is otherwise unknown, at any rate, in genera so widespread as

*Agama*. The author's views on the ancestral form of Agama were based on " considerations derived from a general survey of the family Agamidæ," such data might be misinterpreted if it should happen that the South African species of Agama constitute the most primitive section of all.

## Zoological Areas.

I will not occupy your time by attempting to define faunal areas in South Africa, for the fact that no two groups distribute themselves in the same way makes this a most tantalising pursuit. It is rightly assumed that there must be some correlation between the distribution of animals and of plants, and that in both cases the segregation of species and genera is to some extent determined by geological and climatic factors; nevertheless, any attempt to establish zoological areas comparable to those of botanists would be fallacious. Thus, on vertebrate data we cannot recognise a South-West Cape region like that indicated by Engler and other botanists. So far as I know, not a single family of terrestrial vertebrates is confined to the south-west region of the Cape, and the peculiar genera and species which do occur there have closely related forms in other parts of Southern Africa. Here, too, I may remark that this botanical region is evidently not so sharply defined as one might think from the published maps. It is now realised that sharply defined zoological areas can only occur in regions which are limited by insurmountable physical barriers, here non-existent. Such areas are comparable to Oceanic islands; their faunas have not the slightest value as zoological units, being invariably heterogeneous, with components of diverse origin.

Physical barriers of minor magnitude do occur in South Africa. Such a one is the Limpopo River, which is the northern boundary of several very characteristic genera and species, like the genus *Stasimopus* (trap-door spiders of the family Ctenizidæ), and *Mabuia trivittata* (a very common skink lizard). In the interior, various ranges of mountains tend to isolate faunal districts. Most importanto of such ranges is the Drakensberg, which serves to divide the northern waves of invasion into two streams. But, on the whole, the fauna of South Africa is not separable from that of East Africa. These groups which have entered from the north have their primitive members chiefly in the south and south-west, and their highest forms more or less concentrated in the tropics; the few groups which seem to have radiated from the south have their greatest specialisation in some part of South Africa and more generalised forms in the tropics. At no part of this large region can we say that the fauna is wholly of single origin. Therefore, no useful purpose is served in subdividing the region, except on the distribution of some single group, when the most important primary divisions would be those distinguishing the routes of migration rather than the location of peculiar forms.

## Conclusion.

I take the opportunity of alluding to the fact that our knowledge of animal distribution in South Africa is still most imperfect and such data as we have of a very elementary description. In most groups of animals, the only data yet published are those found in the works of the great systematists; monotonous lists of localities, often without a particle of information to enliven the list. Therein, the name of some town is applied to all places in the neighbourhood, even though highly distinct habitats like forest and karroo may be included, as at Grahamstown. Such lists are thus absolutely useless, when studying the finer problems of distribution and oecology, for the most important data can only be obtained through intensive study of some neighbourhood where two or more related forms are known to occur. Concerning vertical distribution in South Africa practically nothing is known, or at least nothing has been published: and I believe that no one has attempted to work out the life zones of our mountain regions.

We have interpreted the facts of distribution as testifying to the intensity of the struggle between closely related forms; and even that in any natural group the struggle between primitive and advanced types mainly determines their relative distribution. But we have still insufficient data for estimating the importance of the environmental factors in species formation and distribution. One distinguished herpetologist (Dr. H. Gadow) asserts that "the species are the product of their environmental conditions": but, on the other hand, the belief in adaptation as one of the chief causes of the evolution of specific characters is contradicted by Dr. J. C. Willis. I believe that much light on this question could be obtained through an intensive study of distribution on the Drakensberg or other mountain region. In the meantime, though I cannot assert it as an established fact, I do not hesitate to express my belief in the view that species generally have not arisen in the places they now occupy; and that, in its period of dominance a species tends to spread outwards from its place of origin to suitable localities in all parts of the earth, afterwards becoming limited in range chiefly through competition with succeeding higher types, or at any rate becoming replaced by higher types.

In this utilitarian age, when problems of everyday importance receive first consideration, it is stranger still that the distribution of some of our most serious animal pests has not been worked out. The distribution of such actual and potential pests as mosquitos and ticks is only known in vague outline, and scarcely more can be said of the rodents, the most formidable of all mammals. Such an enquiry, one would think, ought to be the essential preliminary to any well-conceived plan of pest destruction or control.

In conclusion, therefore, whilst I fear that some of you may be unwilling to concede the validity of some of my deductions, for you may be impressed with the difficulty of distinguishing between primitive and pseudo-primitive forms, or you may think, as Mendelians do, that all attempts at phylogenetic reconstruction are old-fashioned and should now be abandoned, yet I feel sure you will agree that the study of animal distribution is worthy of more attention than it has hitherto received: for, therein may be found the solution of some of the fundamental problems of biological philosophy. A revival of interest in this and other problems pertaining to animals in their natural environment is needed to restore a proper balance between facts and theories.

## NOTES AND REFERENCES

[1] The following groups of Vertebrates are recorded from the Lower Miocene of Lake Karungu :—Proboscidea, Hyracoidea, Artiodactyls, Perissodactyls, Rodentia, Carnivora, Testudinea and Crocodilia.

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[8] Boulenger, G. A., "Revision of the Lizards of the genus *Nucras*." *Ann. S. African Museum*, XIII.

[9] See Willis, J. C., "Age and Area."

[10] Roberts, A. (1922), "Review of Nomenclature of S. African Birds." *Ann. Transvaal Museum*, VIII.

[11] Boulenger, G. A. and Power, J. H. (1921), "A Revision of the S. African Agamas." *Trans. Roy Soc. South Africa*, IX.