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Dedicated to Mrs. W.S.S. van Benthem Jutting

Periphery and archaic forms

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In many groups the more primitive, more ancestor-like species are living in the periphery of the range of the group. Many authors have regarded this phenomenon as a rule, e.g. MATTHEW, 1915: "Whatever agencies may be assigned as the cause of evolution of a race, it should be at first most progressive at its point of original dispersal, and it will continue this progress at that point in response to whatever stimulus originally caused it and spread out in successive waves of migration, each wave a stage higher than the previous one. At any one time, therefore, the most advanced stages should be nearest the center of dispersal, the most conservative stages farthest from it."

However, in his recent "Animal Species and Evolution", MAYR, 1963, replies to this: "the zoogeographic phenomenon of the survival of primitive types has nothing to do with infraspecific geographic variation. Indeed, the generalization one can make concerning infraspecific variation is precisely the opposite of that of Matthew: the "original" phenotype of a species is usually found in the main body or central part of a species range, while the peripheral populations, particularly the peripherally isolated populations, may deviate secondarily in various ways."

The statement that larger groups have developed out of smaller groups, out of specimens of a single species even, sounds commonplace enough. But then it seems at first sight incomprehensible that two diametrically opposite opinions can exist, the one on infraspecific categories, the other on higher categories, without one of them being false.

In the following pages I will try to solve at least part of the controversy.

"KINDS" OF PERIPHERIES

One of the main reasons for controversial opinions on peripheral species — especially when we include peripheral populations — is the fact that there

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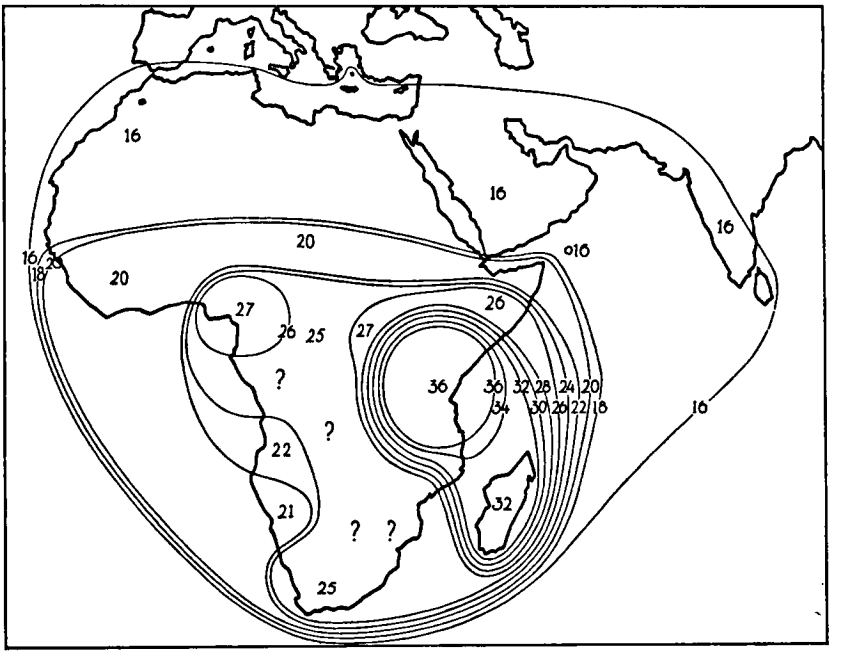
are so many kinds of peripheries. Roughly we can distinguish the following types:

1. The ideal type. Ecological circumstances which are in all directions the same. The periphery of the range of a species will be an expanding circle. If the ecological circumstances are the same indeed in the centre and in the periphery, the central populations will increase just as much as the peripheral ones. The result will be that the population-density will be highest in the centre, gradually decreasing towards the periphery. Because more specimens will move centrifugally from the centre towards the periphery than centripetally, the resultant gene flow also will be from the centre towards the periphery.

   In reality this Willis-like scheme will be approximated only very seldom, were it only because in general the ecological circumstances are not the same in all directions. But in many cases we are able to recognize at least the principle of a centrifugal dispersal, coherent with a centrifugal gene flow.
2. The periphery of a distribution may be there where the species, or larger group, meets with the ecological minimum, where the animals live in *marginal* circumstances (see MAYR, 1963: 392, note). In this case the selection in the periphery will be quite different from that in the centre, which may result in deviating adaptations. On the other hand, in marginal situations propagation takes more time than in the more central, optimal situations. It often takes longer to become adult and so does the development of eggs or young. Though the number of mutations may be the same as in the centre, the exchange of the new possibilities throughout the population will be slower. The resultant adaptive evolution will therefore be slower too.
3. The periphery may be fixed by some absolute barrier. For instance land-animals will find such a barrier at the sea. In extreme cases this periphery may partly coincide with the centre of dispersal. For instance if we consider the distribution of *Bombina bombina* (and most European amphibians possess a comparable pattern) the Balkans may — purely geographically speaking — be regarded as periphery of that distribution, as well as Zuid Limburg in the Netherlands. But when we take into account the geological history of Europe, the extension of the glaciers of the ice-ages etc., it is clear that in the historical sense Zuid Limburg belongs to the periphery, the region last reached by the species, and the Balkans are the centre of dispersal (see MERTENS, 1928).

   Within a larger group we find this kind of distribution in the genus *Chamaeleo* (see map 1). Taking into account the distribution of the main characters (HILLENIUS, 1959) much evidence is found that the centre of dispersal lies in East-Africa (Kenya and Tanganyika). Purely geometrically speaking the periphery of the distribution of this genus is everywhere along the coast of Africa and from Arabia eastward. It is clear that when we use periphery in the geometrical sense of the word, we will find the most contradicting facts concerning the peripheral populations.



MAP 1. Africa and adjacent countries. The geographical range of the genus *Chamaeleo*. The distribution of the main characters. Isopseferes, lines bordering the regions with the same number of of characters. Most probably East Africa (Kenya and Tanganyika) is the centre of distribution. (HILLENIUS, 1959. Drawing by J. A. Mastro).

This is not a hypothetic problem. MAYR (1963) mentions a case (Goldschmidt, 1956) of a "population of *Drosophila subobscura* from Israel (near the southern periphery of the range of this species) that has a richer variety of gene arrangements (26) than any European population studied (14—21)". This in contrast to many similar cases in which the number of gene arrangements is largest in the centre, decreasing to the periphery of the range. As many smaller animals and plants have populated or repopulated Europe, coming from Spain, Italy, the Balkans or Asia Minor, it is not improbable that the Israel population of *Drosophila subobscura* is the remnant of an original centre of distribution of this species and that the European populations, though now ecologically favored, belong to the periphery of the distribution.

Centre of distribution is generally taken in the historical sense, as the source of the present range. If we take periphery as the opposite of centre, we also must differentiate between periphery in the geometrical and in the historical sense.

Although it will not always be possible to find some evidence on the history of a species or a group of species, I am sure that many contradic-

tions about peripheral species or populations will be solved if we separate the geometrical periphery from the historical.

4. Islands form a special kind of periphery. If they lie on more or less equal distances from the mainland they may approximate the first kind of periphery. But when they lie in a chain extending from the mainland, the islands which are farthest away will be populated last. Every island will be populated by only a few invaders (apart from some cases of flying animals, birds, insects, bats), which can take with them only a limited part of the total genetic variability of the species. The last island in the series will receive only a very poor genetic material.

The great difference between the first and the fourth kind of periphery is that each peripheral population in the first sense will have originated from central populations, independantly from other peripheral populations, whereas the populations on the last island of a chain of islands extending from the mainland, may all be derived from the same few invaders. In the first case we will find the phenomenon that MAYR describes (1958: 158) "The phenomenon of conspicuous divergence of peripherally isolated populations, so well illustrated by the *Tanysiptera hydrocharis-galatea* group ... familiar to every taxonomist. Scores, if not hundreds, of examples can be found in every monograph or checklist."

In the other case we may find perhaps a relation between the peripheral populations within a species and peripheral species or genera within a larger group.

EXAMPLES OF ARCHAIC AND PERIPHERAL FORMS

In addition to the famous cases of *Sphenodon* and the Leiopelmidae we may mention the following cases: TIHEN (1949: 599) — "As is true in several reptile groups, the evidence in the case of the Gerrhonotinae points to the northern Mexican plateau as the center of dispersal. At the present time only the more specialized forms of the group are found in that region; the more peripheral forms exhibit a progressively greater number of primitive features, corresponding closely with their distance from the assumed center of dispersal. In some cases forms at the opposite peripheries of the range show a strong resemblance to each other in certain primitive characters not found elsewhere in the group, even though other features in each form may have been so modified that generic separation is warranted."

According to WILLIAMS (1952) *Testudo radiata* of Madagascar and *T. gigantea* of Aldabra belong to the oldest group within the genus *Testudo*, together with species that lived in the eocene.

According to WESTPHAL (1958) the recent giant salamanders of east Asia (*Megalobatrachus*) belongs to the same species as *Andrias scheuchzeri* from the Tertiary of Europe.

MCDOWELL & BOGERT (1954: 134) on *Lanthanotus borneensis*, the rare lizard of Northern Borneo: ... structural resemblanches between *Lantha-*

notus and *Varanus* are found to be both numerous and important. However, it is shown here that there is still greater affinity between *Lanthanotus* and three Cretaceous families believed to be closely related to *Varanus,* the Aigialosauridae, Mosasauridae, and Dolichosauridae.

TAYLOR (1935: 154) on *Eumeces longirostris* of the Bermuda's (the other species of this genus live in North America, North Africa and Asia Minor, Southeastern Asia and some of the continental islands of this area): "It may be regarded as a form contemporaneous with the ancestors of the present *Fasciatus, Anthracinus* and *Skiltonianus* groups, that has maintained its primitive characters due to its long sojourn in an environment that has in all probability changed but little since its arrival."

In THENIUS & HOFER (1960) we find several examples of primitive mammals living in peripheral areas:

On page 160—161: "Unter den echten Bären (Ursinae) ist der Malayenbär (*Helarctos*) der ursprünglichste, während die Braunbären (*Ursus arctos*) zu den fortschrittlichsten und auch geologisch jüngsten gehören."

On page 169: "... die Madagascar-Mungos mit *Galidia, Salanoia* und *Galidictis* als Galidiinae. Letztere besitzen durch verschiedene herpestesähnliche Merkmale ... eine Art Mittelstellung zwischen den Herpestiden und Viverriden. Es sind altertümliche Formen, wie dies auch für andere madagassische Arten gilt."

On page 170—171: (on *Cryptoprocta*) "Es handelt sich um einen sehr konservativen Überlebenden des ältesten, viverridenähnlichen Stadiums der Feliden, welcher der oligozänen Gattung *Proailurus* nahesteht und frühzeitig von dieser Form abgezweigt ist."

On page 231: "Die Zwerghirsche bilden eine gegenwärtig nur durch zwei b.z.w. drei Gattungen (*Tragulus* und "*Moschiola*" sowie *Hyemoschus*) auf Reliktareale (Südostasien, Westafrika) beschränkte Gruppe, die im Tertiär in ganz Eurasien und Afrika verbreitet war."

On page 243: " "*Anoa*" *depressicornis* bildet jedenfalls die kleinste und primitivste Art der Gattung *Bubalus.*"

Some cases seem to deviate from this general pattern. For instance, the muskdeer (*Moschus moschiferus*), belonging (THENIUS & HOFER, 1960) to the most primitive deer, lives in East Asia, whereas the oldest fossils of this genus are found in the pliocene also in East Asia. But the recent muskdeer live high up in the mountains, in summer generally above 2500 m. This inhospitable region may well be regarded as a periphery in the vertical sense. (The recent giant salamanders live also in the mountains, whereas the tertiary relative lived in shallow waters in the plains.)

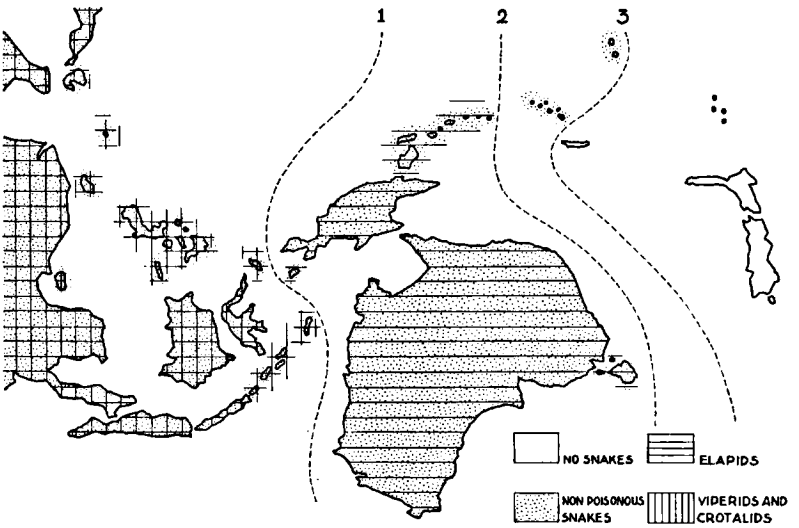
POSSIBLE EXPLANATIONS

1. The most simple explanation of the occurrence of older forms in the periphery is the fact that older forms naturally started their dispersal earlier than forms that developed later. The chance that succesful higher forms develop is higher in places where competition is strongest, i.e. in the areas

with the densest population. In general this will be in areas with optimal ecological circumstances. If there are no great geological and ecological changes, the source-region of new forms will not change much. Then, indeed, we have a chance to get a distribution pattern based on successive waves, of which the first are more primitive than the latter.

A fine example of this kind is given in the distribution of the snakes. Roughly the snakes can be divided in non-poisonous snakes, poisonous snakes with unmovable fangs (elapids and seasnakes) and poisonous snakes with movable fangs (viperids and crotalids). The development of poison is probably to be regarded as a later perfection within the group of snakes. The development of movable fangs is to be regarded as a later perfection within the group of the poisonous snakes. So the sequence non-poisonous, elapids, crotalids-viperids roughly indicates a sequence from older to newer forms.

Non-poisonous snakes reached almost all parts of the world (unless the climate was too cold). They even reached the Galapagos-islands, Madagascar, the Balearics, Corsica, Sardinia, many of the Antilles. Of the greater islands only New Zealand and Hawaii were not reached.



MAP 2. The distribution of snakes in the region southeast from Asia. The non-poisonous snakes, which have to be regarded as the oldest snakes, have not passed line 3, the next old forms, the elapids, have not passed line 2 and the newest forms, the viperids and crotalids, have found their limit in line 1. (Drawing by J. A. Mastro).

Elapids live on the great continents, Indonesia, New-Guinea and Australia, but they did not reach the Galapagos, Madagascar, Balearics, Corsica, Sardinia, Antilles. Viperids and crotalids reached Indonesia, but not the eastern, Australian part of it, they also did not reach Australia nor any of the above mentioned islands (KLEMMER, 1963).

In map 2 the south-eastern part of this distribution is shown. In this case we see that the older forms, though living in the periphery, need not necessarily become extinct in the more central parts of the distribution. Perhaps this is only possible when the successive stages are not too closely related, because otherwise the competition will exclude the possibility of several stages living together.

2. Closely connected with the first explanation is DOBZHANSKI's remark (1951: 134): "... the longer a territory is occupied by a species the greater will tend to be the adaptive polymorphism and the variability in populations. Conversely, at the margins of its distribution area, unless the species is stopped by an insuperable geographic barrier, it is likely to have a toehold in only few ecological niches. A limited adaptive variability is likely to characterize marginal populations."

This argument is valid for populations within a species as well as for higher categories: the later a population or species will arrive in an area, the less time will be available to obtain adaptations, the less deviating these animals will be from the original immigrants.

This does not explain why peripheral animals, which have just as long a history behind them as the central relatives, would have changed so much less (see 3 and 4).

3. Apart perhaps from birds and other flying animals, which, coming from the centre, may have reached in one flight the periphery, animals going from the centre towards the periphery pass through many different environments. If the dispersal takes many generations, it is possible that in every new environment new adaptations will be obtained, soon to be lost when next generations go further, through different environments again. But it is clear, that if a species, or a group of species, is able to continue its expansion, these adaptations will be rather superficial. It is improbable that animals would become specialized for the living in water, then change into a desert-animal, then become adapted to the life in forests or moors and so on. Most probable the animals that are able to continue emigration are the less specialized, less adapted, i.e. the animals that are closest to the original type. This sounds like a variant of Cope's law "the survival of the unspecialized". Indeed, I think there is not much difference between animals that have passed from centre to periphery through many different climates and other differences in ecological circumstances, and animals that have been able to stand the same changes that occurred in the same place in the course of history.

4. In point 3 we spoke about less specialized animals that always *could* continue their way. Perhaps in many cases we have to change this *could* by *should*. In other words, the animals that could not adapt themselves to new surroundings *had to* continue their way. Animals that are able to adapt themselves to new surroundings will most probably stay there. Those that do not obtain the necessary new characters will be forced by competition to emigrate or to die.

There is some evidence of the existence of genes that lower the mutation-

rate of other genes. It is not unthinkable that these "braking" genes, that are of disadvantage in the competition with normally developing relatives, will be of advantage in emigrating groups. Perhaps such brakes on the speed of evolution may be considered as adaptations to emigration (off course, this will be only possible in cases of very slow emigration).

5. When the periphery of a distribution coincides with the ecological margin (this is often the case) we also will have a retardation in adaptation, as is discussed under point 2 of the kinds of periphery.

6. In the ideal type of periphery, in which there is more centrifugal gene flow than centripetal, more new characters will come from the centre towards the periphery than the other way round. Though evolution need not stand still at the periphery, the most effective new characters, brought about by the competition which is stronger in the denser populated centre than in the periphery, will show a centrifugal dispersal.

Now we must try to reconcile the opinions of MATTHEW and MAYR, as cited in the opening of this essay.

In Dobzhanski's remark (explanation 2) we found already an argument that is valid both for populations within the same species as for species or higher categories. „The phenomenon of conspicuous divergence of peripherally isolated populations" (MAYR, 1958) may then be explained as follows: the peripheral populations, possessing only a poor genetic background and coming only quite recently (peripheral in the historical sense) in their range, can only have obtained superficial adaptations or even only accidental modifications. Compared with the radical specializations that in the course of time may be brought about in the competition of the central populations, the divergence of the peripherally isolated populations will be of a minor order. In the wording of Mayr's objection against Matthew we may see perhaps a clue towards a solution: it is the *phenotype* of the central populations that is more original than that of peripheral populations. Most authors agree that the genetic base of central populations is much richer than that of peripheral populations. As long as the central populations are not isolated from each other the resultant phenotype will tend to be conservative, because of the conformistic tendencies of populations with much gene-exchange. But as soon as the central populations are isolated, by geographical barriers (as in Spain and in the Balkans) or by differences in chromosome-patterns (HILLENIUS, 1963), the richness of the genetic material becomes visible in clearly different phenotypes, in clearly definable subspecies (as is the case for many amphibians in Spain and in the Balkans) or even different species (as is the case when the chromosome-patterns differ in such a degree as in the genus *Chamaeleo*).

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