THE FORMENKREIS-THEORY.

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THE Formenkreis theory is believed by many to be a German invention, of whose essence and significance many systematists have not yet received a clear impression. One point, particularly, has not yet become clear to them, i.e. whether there is a difference between the species conception of the modern systematist and the Formenkreis theory and, if such exists, what that difference is. Many people are of the opinion that the origin of the Formenkreis theory is closely connected with the use of trinomial nomenclature. In this connection it might be of value to give a short historical review.

Very soon after Linné had introduced the binary naming of living organisms, the opinion was emphatically expressed that not all the forms separated in that manner were of equal value. The great philosopher, Kant, in the course of his lectures on physical geography given in 1775 points out that we must discriminate between *natural description* and *natural history*. He calls the first the *artificial* system by division into classes which are arranged according to resemblance, and calls the latter the *natural* system by division into tribes which are arranged according to the relationship of the animals. He speaks, for example, of the squirrel, which is brown in Germany, but becomes gray in Siberia, and of birds of the same species which vary in color in different climates. Some years afterwards, in 1791, another German, Esper, in a treatise on varieties, points to the fact that there are some genera which contain so many and so closely related species, that it would be advisable to subdivide them. Some of the varieties, he goes on to say, are characterized by essential characters, and he proposes to call them subspecies. That these subspecies have been derived from the species is shown, according to Esper, by the perfect similarity of the essential characters.

George Cuvier, in 1798, tried to give a definition of a species and what he calls varieties, in the following paragraph:

> "If the descendants of some organisms have more or less deviated from the appearance of their ancestors, one says they have varied. It has been observed that the most variable characters of organisms are size and color. The first depends mainly on the quantity of food, the latter on the influence of light and other causes so obscure that color often seems to

* An address delivered before the Naturalists' Forum of the Academy of Natural Sciences of Philadelphia on January 28, 1936.

differ only by the action of chance. However, the variation of both these characters has certain limits, which can be determined by observation. To accept two creatures, which differ more or less, as being only varieties of one species, it is necessary firstly that the distinguishing characters belong to those which are known to vary; secondly that there should be cause for variation; and thirdly that they should produce fertile offspring when crossed. Therefore two wild forms which live at the same place in the same climate, without interbreeding, and always maintain their differences, have to be regarded as different species, no matter how trifling the difference might be."

This sounds like a very modern definition, although it dates back to the end of the 18th century. This is followed by a period, during which the use of the term variety to characterize slight deviations from some other type, already named, became gradually discarded, although authors continued to distinguish by binomials a score of forms which only differed in small degree. As a reason for this practice, followed until quite recently in many branches of zoology, Friedrich Boie in 1831 gives the following: "It is not advisable to subordinate living beings under other species, if they differ from the latter by constant characters recurring in subsequent generations, for, it seems highly probable that there exist merely genera, in which all species merge into each other by such imperceptible gradations, that there can be no longer any question of subordination. A variation traceable through generations should be ranked as a full species, unless it can be shown that such variation returns to the original form from which it appears to have deviated."

This view very soon met with strong opposition on the part of other German ornithologists. Friedrich Faber was one of the foremost. In 1825 he claimed that the different species, created by Nature from the very beginning, would vary in shape and color when extending their range of distribution, under the influence of a new environment. These were the variations or races, which some of his contemporaries were inclined to treat as separate species. He continues: "If we accepted all these local variations as distinct species, no natural system would finally be able to hold them, no ornithologist to put them in order, no memory to retain them. Research into the laws of geographical distribution of birds would become blocked at its source, and the foundations of science itself would be shaken." This met with approval from many ornithologists, such as Bruch, Naumann and others. In 1833 a book wholly devoted to this subject appeared, written by Constantine Gloger under the title "Das Abändern der Vögel durch Einfluss des Klimas" (The Variation of birds under climatic influence). Here Gloger tries to draw a sharp line between true species and climatic varieties; in his opinion, the latter did not deserve to be named at all, or,

if they were, they should be expressly marked as such. To invent, however, the simplest method of doing so was left to Hermann Schlegel. In his treatise "Kritische Uebersicht der europäischen Vögel," published at Leiden in 1844, he first applied trinomials in the way we do now by simply adding the subspecific name to the name of the species. This was in his day quite a revolutionary procedure; one had become accustomed to look upon Linné's binomial nomenclature as a scientific principle not to be disturbed, and very few people therefore dared to follow Schlegel.

Schlegel's trinomial nomenclature had first to win approval in America before it found any acceptance among Old World ornithologists. John Cassin, in 1854, was the first American who endeavoured to adopt this novelty; but its chief promoter in this country was Spencer Fullerton Baird, who, from 1858 onwards, made use of trinomials on a large scale, although, by intercalating the term "var.", in a somewhat "milder" form. He soon acquired quite a number of followers, and when, in 1886, the American Ornithologists' Union laid down their "Rules for Zoological Nomenclature," the use of trinomials was recommended by the Committee. Henceforward, trinomialism was regarded in Europe as being an American innovation, which in the beginning was looked upon with suspicion, and furiously attacked, as soon as it was noticed that some Old World authors began to introduce it in their writings (as Sewertzow in 1876, Count Berlepsch in 1881, Seebohm in 1885 and Ernst Hartert in 1887). But all the hostility of the Old School has not succeeded in blocking the reform, and the last defenders of binomials are trying to hold a fort which was practically surrendered some time ago.

So finally the moment seemed to have arrived when both contending parties, the Synthetisists and the Analytists among bird students, would shake hands, having been reconciled by the adoption of a new method. But soon it became apparent that the reconciliation was only a formal one, and that there was great diversity of opinion regarding the essence of this new method. Faber and Gloger accepted the theory that there was but one certainty, namely the external integrity of the species, this being, so to say, the axis, round which the varieties of the same species would whirl in perpetual movement; if one let go this axis, even the spectator would grow dizzy —to quote the instructive expression of Gloger.

But after the appearance of Darwin's book on the Origin of Species, in 1859, this view gave place to a very different one. For Darwin and his adherents there existed no other difference between species and varieties than the fact, that the varieties are known or believed still to be connected by intermediate linking forms, whereas the species were formerly connected with each other in this way. There seemed, therefore, no longer any reason for accepting the sharp boundary line drawn by Pre-Darwinists to separate

the species, and therefore only one criterion for the determination of species and subspecies seemed to hold good: the degree of morphological difference. This had clearly been recommended by Darwin himself, when he wrote: "two forms, if differing very little, are generally ranked as varieties, notwithstanding that intermediate linking forms have not been discovered. The amount of difference considered necessary to give to forms the rank of species is quite indefinite." Taxonomists, as far as they decided to adopt the introduction of subspecies, now began to look at the whole question as being simply a technical one, as being a matter of convention and not one of scientific principle. Joel Asaph Allen, in 1871, was the first to propose, that intergradation should be regarded as the touchstone of trinomialism. Owing to Allen's high influence among vertebrate zoologists in this country, this suggestion met general approval in America; but the method very soon degenerated, because it became handled with orthodoxy and red tape. Those who claimed to belong to Allen's truest followers, gave every form the rank of a full species unless intergradation with another one was fully proved, slight as the differential characters might be. All island forms, for example, were on principle treated as species, because intergrading was out of question in cases of complete isolation of a given community.

In Germany, the Darwinian influence led ornithologists in quite another blind alley. During the last twenty years of the 19th century, the leading German ornithologists agreed to regard the degree of differentiation as being the only test to decide the question. In 1891, the German Ornithologists' Union (Deutsche Ornith. Gesellschaft) accepted the following paragraph among the rules of zoological nomenclature: "If given local forms differ from each other only in such a slight degree by color, or by size or shape, that any diagnosis would be of no use for determination unless direct comparison were possible or unless one knew the locality, such local forms should not be treated bionomially as species, but should be marked as subspecies by attaching a third name to the name of the species, from which the subspecies has branched off." The application of this rule soon turned good into bad. German ornithologists started to treat all very similar looking forms as subspecies, for example the European Willow Tit became a subspecies of the European Marsh Tit, *Certhia brachydactyla* became a subspecies of *Certhia familiaris;* and, on the other hand, one single striking difference in coloration was regarded as sufficient to treat two forms, otherwise quite alike and even interbreeding at the borders of their range, as full species; for instance the Carrion Crow and the Hooded Crow, or the British and the Continental White Wagtails. Gloger's chains of connected forms thus became dismembered again, and their parts were thrown pell-mell. The confusion had reached a new climax.

Such was the state of affairs when in 1897 Otto Kleinschmidt, after

thorough taxonomic studies, went on to demonstrate the failure of the method then in vogue. By examining the variation that exists in the Marsh Tits and the Crested Larks he had discovered the existence of two very similar species, living side by side in a considerable part of their range and showing some parallelism in their geographic variation. Kleinschmidt then had gone through the literature and thereby revealed the fact, that Christian Ludwig Brehm, one of the Pre-Darwinists, already had disentangled the matter in a very able way, and that it had been their interpretation of Darwin's doctrine which had led the next generation to mix things up again. It is this experience which started Kleinschmidt's passionate opposition against Darwinism. The more deeply he went into the matter of geographic variation of animals, of birds and butterflies, the more intense became his belief that there was no proof at all to support the Darwinian ideas. On the contrary it seemed to Kleinschmidt that every species always remained separated from all other species by a gap, if one tried to follow the descent as far back as paleontological testimony allows, and therefore he turned back to the view that every species had its own independent origin. According to Kleinschmidt, species are undergoing a certain, in some cases a very considerable amount of geographic variation, but none of these geographic races can ever be regarded as incipient species. It is the task of the taxonomist to discover the limits of the true natural species by tracing all the geographical races into which they have split. In order to distinguish by name these so-called "natural species" from the species of the Darwinian school, Kleinschmidt introduced the term "*Formenkreis,*" but there is not the slightest difference between his "formenkreis" and the "species" of Gloger and certain other Pre-Darwinists.

Let me quote his own words, from the English translation of his textbook which appeared in 1930 under the title: "The Formenkreis Theory and the Progress of the Organic World." "The Formenkreis Theory upholds the indications found in Nature as to independent sources of life; on the other hand the limits of each independent group are widened to an inconceivable extent. If the question is asked: May there not be a relationship between root and root? I would reply: Yes! If it is granted that this is quite a different kind of relationship than between two leaves springing from the same root, and in the same way that one can detect a relationship between drops of water falling in succession from two adjoining spots, or even from a single spot of the same rain soaked roof.

"There was a time which, on account of its temperature and chemical conditions, was favorable for the origin of organisms upon the earth. So long as this period lasted, the foundations of the Formenkreises continued to come into existence and the Formenkreises themselves continued to arise through differentiation. That such a period existed, as well as further

progress of life, is the work of the Creator. Theology consequently has no desire to borrow from science in order to explain the origin of life.

"Some of the Formenkreises developed rapidly and then became rigid (Lingula). Some of them took to growing slowly and reached a higher development. Many spread as far as their organization permitted, over the greater divisions of the earth or seas, some being cosmopolitan with few races, others residents with many races.

"Our aim is no longer systematic arrangement (as a demonstration of the degree of morphological differences), but research on origin and descent (that is to say, the active process of growth). The common origin gives the Formenkreis a concrete existence, whereas it would be a mere abstraction as a product of Taxonomy. To put it quite shortly: The novelty of the Formenkreis Theory is its extension beyond the idea of groups of subtle forms, to the investigation of questions of relationship and origin and the connection between taxonomy and the theory of descent.

"It is no longer the varying degree of difference which marks the distinction between species and a race, but the plain answer to the question, whether there is geographical replacement and exclusion or not.

"Not only subtle forms, which are very similar to each other or which are connected by intergradation, but also good species of the old taxonomy, in spite of striking external dissimilarity or considerable gaps in their continuity, will be included in the same Formenkreis."

Kleinschmidt summarizes "Each Formenkreis has probably an independent center of origin, an independent period or origin, and an independent progress accompanied with an independent rate of development, or in a word, an independent existence."

During forty years of research work, Kleinschmidt has not materially changed his ideas. Let us now consider his influence on the development of taxonomy.

This influence can hardly be overestimated. The present day use of Trinomialism, not only in ornithology, but in many other branches of zoology too, is mainly based on Kleinschmidt's views. Ornithologists became more and more accustomed to the idea that there was really something like natural species, surrounded by sharp structural boundaries; and even though many of them soon became aware of the fact that the essence of the Formenkreis theory would not bear every test, most of them handled the matter *as if* they believed in natural species, by including more and more geographical representatives in one species compound. To use a metaphor: present days taxonomy can be compared with one of the Indian Banyans. As long as they are young, they need the support of some strong rigid tree, but by and by they develop innumerable roots of their own round this center, and at the end the supporting tree is suffocated, and what remains

is a majestic *Ficus* tree, standing at the place of its former host and even mistaken for it by the casual observer. Most scientists who now use the practice proposed by Kleinschmidt are Darwinists. They call the species by the name of Formenkreis, not because they believe in the independence of species, but because it proved to be advantageous to adopt such a fiction.

In how far is this advantageous? How can it be that a scheme works all right which is based on an erroneous supposition? I believe the reason for this to be the fact that most of the present day species are much older units than one had formerly accepted, and that it is practically never the individual variation occurring *within* a population which gives rise to speciation. On the contrary, species usually multiply only on the basis of geographic variation, and this is a very slow process. One of our critical tests of taxonomy, in fact the only one which can be adopted for practical use, is furnished by geographical distribution.

We are used to call two similar forms subspecies of one species, if they replace each other in space; and we call them different species whenever they live in the same area without interbreeding. But by doing this we shall always have to remember, that this is only one way to treat the matter, one of great convenience to the zoogeographer and the ecologist, but it is nevertheless an *artificial* system, not at all doing justice to the degree of differentiation. It is pretty certain that many geographic representatives at present regarded as subspecies would behave like so-called "true species" if nature gave them a chance of settling in the same area. In a few instances we get a surprising proof of this. It most frequently occurs with island birds. Every taxonomer will know, from his own experience, some instances of two closely allied and vicarious forms meeting again somewhere and living there together without interbreeding. I may mention here the puzzling *Collocalia* group, or the Kingfishers of Micronesia and Melanesia. Nobody had the slightest doubt that *Parus major* and *Parus minor* were strictly representing each other, until both were found to inhabit together a large area in the Amur land. There are other and even more puzzling cases. The English Sparrow *Parus domesticus* and the Mediterranean Willow Sparrow, *Passer hispaniolensis*, live side by side in Spain, in Greece, in Asia Minor and in Palestine, somewhat differing in ecology. Here they never interbreed and everybody would treat them as species. But if we proceed to Northern Africa, we will meet there a mixed population, practically composed of hybrids only. Here they behave exactly like two members of one species. What to do with them?

These are not the only facts, which drive the Formenkreis Theory into a corner. Take the following. It is a pretty well grounded assumption that subspecies of one species will differ only to a slight degree or not at all with regard to life history, as opposed to what distinguishes true species. Ecology,

therefore, has become an important help in taxonomy. But how to handle cases like this: In Melanesia you will find a Thrush of the group *Turdus papuensis* living in the alpine grass-plains of the high mountains of some of the Solomon Islands. Here this bird is a very typical highland bird, never coming down to the lowlands. By proceeding towards the East, you will get to flat islands only, and here practically the same bird lives at sea level, under extremely different climatic conditions. Or examine the bird fauna of New Guinea. In the high mountains of this island, you will encounter several birds very closely related to lowland forms of the same district, yet constantly differing, mostly by larger size, but also in some other respects. Intermediates do not occur. Shall these mountain forms be treated as subspecies of the lowland species, or do they merit the rank of a full species? That is just a matter of taste. In these cases, at least, lowland and highland forms do not differ any more from each other, or they differ even less, than horizontal representatives often do.

Should we, in view of shortcomings like that, discard altogether the scheme to which the Formenkreis Theory once had encouraged taxonomy? I think that would be a deplorable mistake.

We shall always have to take into consideration that life never can be forced into a rigid system; but of all systems ever proposed the present day use of trinomials is the least evil, in spite of some deficiencies. To return, for safety's sake, to some more cautious use of trinomials would be a decided backstep. May I quote, in justification of our present-day procedure, once more Constantin Gloger, who, 100 years ago, wrote the following sentence: "It is only by connecting the facts that we shall be led to the principal laws, but not by splitting and dismembering. The splitter separates homogeneous and corresponding facts, and throws them separately upon the unarranged heap, where they will escape the attention of Science which tries to arrange them in a true and natural order; and so they will remain in disorder, having lost all their meaning with regard to the whole and being placed themselves in a wrong light."

Whoever uses trinomials in a modern way, will have to be gifted not only with knowledge, but also with tact and last but not least with *moderation.* It is sometimes more misleading than helpful to rank very widely differentiated forms as subspecies, only on account of obvious affinity to some geographic representative. No fast line can be drawn here. But one ought to refrain from red tape. Whoever wants to hold to firm rules, should give up taxonomical work. Nature is much too disorderly for such a man. He better would turn to collecting postage stamps.

May I draw your attention, in conclusion, to the nomenclatural scheme introduced some years ago by Bernhard Rensch. He proposed to discard the term Formenkreis, unless one believed in independent species. The

more or less large racial compounds of modern ornithology he calls a *Rassenkreis* or a Circle of Races, and if one group of geographic representatives can be subdivided into two or more sharply defined minor groups, he proposes *not* to rank them all together as subspecies of one species, but to break up the compound into several Rassenkreises or Circles of Races, which represent each other geographically and apparently are of common origin, forming what Rensch calls an *Artenkreis* or Circle of Species. It is not the task of *nomenclature* to express all systematic judgment, it must suffice that it expresses the *essential* part of it, and we should always be careful not to overdo. Trinomialism cannot express our view as to which Circles of Races constitute a Circle of Species. We should gladly leave this to the monographer of the genus who can do this in his tables.

It is one, and perhaps the chief, aim of present day nomenclature to support our overburdened memory, and this will be attained by adopting large genera and large circles of races, both, however, without exaggeration.

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January 16, 1936.