most recent great migration; it has profoundly affected zoögeographic conditions; it is the one where our data are most complete and accurate; we can perceive its causes and conditions most clearly, and we have a great deal of corroborative evidence in history and tradition.

FIGURE 6. Dispersal and distribution of the principal races of man
No attempt is made to indicate anything beyond the broader lines of dispersal.

((Most)) authorities are to-day agreed in placing the center of dispersal of the human race in Asia.[39a] Its more exact location may be differently interpreted, but the consensus of modern opinion would place it probably in or about the great plateau of central Asia. In this region, now barren and sparsely inhabited, are the remains of civilizations perhaps more ancient than any of which we have record. Immediately around its borders lie the regions of the earliest recorded civilizations,—of Chaldea, Asia Minor and Egypt to the westward, of India to the south, of China to the east. From this region came the successive invasions which overflowed Europe in prehistoric, classical and mediæval times, each tribe pressing

[39a. Recent discoveries by Dr. Robert Broom show the presence of very primitive hominids in South Africa.—E.H.C.]

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Sven Ekman

pelagic types show a more pronounced benthal origin, thus the group Pelagica among the nemerteans, since epipelagic nemerteans are absent; the genera *Melanoteuthis* and *Cirrothauma* and the families Bolitænidæ, Amphitretidæ and Vampyroteuthidæ among the otherwise mainly benthal octopodid squids; the Pelagothuriidæ, which represent the only pelagic type among the echinoderms, and some fish families, namely the Ceratioidea, Saccopharyngidæ and the pelagic members of the Apoda. The nearest relatives of these fish are true bottom forms which partly belong to the deep sea and partly to the shelf.

We now turn from the biocœnotic to the regional origin. Because of the cold-water character of the bathypelagic fauna we might incline to the view that this fauna derives for the most part from the arctic and antarctic pelagic fauna. But this cannot be true since the polar pelagic faunas are considerably less rich in species than that of less cold regions. It is in these latter regions that we must look for the original home of the greater part of the bathypelagic fauna. This has been borne out by phylogenetic investigations on radiolarians[203, 417] and several metazoan groups. Theoretically, a polar origin is occasionally conceivable, for instance in connection with an equatorial submergence of a polar species.

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CONCLUDING REMARKS

In the course of this work I have often had occasion to stress that as a characteristic of a zoogeographical region an endemic family is more important than an endemic genus, an endemic genus more important than an endemic species, and that endemic elements are more important than those which are common also to neighbouring regions. We must now devote further attention to these methodological questions.

The taxonomic (morphological) differences between two closely related genera are more comprehensive than the differences between two species of the same genus, and palæontological discoveries show that the generic differences have taken a longer time to develop than differences between species. In general, the endemic genus of a region has thus lived a longer time in the environmental conditions of this region than an endemic species in the environment of *its* region. The same is true of an endemic family as compared with an endemic genus. There is, therefore, in general a parallel between the taxonomic rank of an endemic element and the time it has lived in the environment in question. The "environment", of course, does not apply to regions with purely geographical delimitation, for

instance by certain longitudes and latitudes, since these have often been subjected to climatical and other alterations, but to the ecological conditions to which the species (genus, family, etc.) is adapted.

The taxonomic scale contains, therefore, historical documents of great zoogeographical value. It is important in this connection that for close on 100 years taxonomy has operated mainly with phylogenetic, that is to say historical, concepts.

The surest basis for a historical zoogeography is clearly provided by palæontological, palæogeographical and palæoclimatological evidence. This is available to a certain extent and has been drawn upon in the preceding chapters. But as is well known, palæontology is by no means free from gaps and here taxonomy thus can provide a welcome complement.

Another factor which deserves special attention in the characterization of a fauna is endemism. Because of its exclusive occurrence within a environmental region a greater value must be attached to an endemic than to a non-endemic species, genus, etc., in the characterization of this region. We may imagine, for instance, an endemic genus with five species all of which are thus endemic in the same region. This genus will clearly be more characteristic for this region than another genus which likewise possesses five endemic species within the said region, but has some species in other regions as well. The same criterion must also be applied to an endemic family as compared with a non-endemic family. That an endemic species is more characteristic for a region than a species which is also found in other regions, is obvious.

The characterization of zoogeographical regions and the assessment of their relationship to one another results in a regional zoogeographical system with a graduated scale of super- and subregions. The parallel with the taxonomic system and its scale of classes, orders, families, etc., is clear. And just as the final aim of taxonomic research is not the graduated scale *per se* but the unravelling of the historical (phylogenetic) relationships between the taxonomic categories and thus the history of the animal kingdom, in the same way the final aim of zoogeography is not the graduated regional system in itself but the history which this system reflects, that is the history of the faunas. Zoogeography, like other sciences, strives to discover the ultimate causes. And the causal connections here are, as in so many other cases, to a great extent historical connections. Hence the importance of the parallelism between the rank of a region within the zoogeographical system and the position of its faunal constituents within the taxonomic scale.

To this must be added yet another factor. In the assessment of the

position of a fauna within the zoogeographical system, that is to say its greater or lesser independence as a centre of development, we may introduce mathematical values for its various elements according to age within the environmental region, endemism or other facts, and these values may be combined into more comprehensive figures by summation, multiplication and division. This offers considerable advantages. For there is a fair number of partial values, which must be graded and combined so as to arrive at a reliable estimation: the value for families, genera and species in comparison to one another, the value for endemism and non-endemism in various taxonomic elements, the value for affinity with other regions as compared with independence, etc. It is advantageous to have a statistically expressed survey in order to be able to summarize the many combinations and so reach as far as possible an objective estimate instead of a more or less arbitrary and subjective one. The basis for such a statistical estimate is, of course, a fully adequate faunistical knowledge of the group or groups of animals with which this analysis is concerned. Space precludes a detailed description of the method. For this I must content myself with a reference to an earlier paper.[147]

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Like all other biological phenomena, geographical distribution is the product of an interaction between two factors, namely the physiological properties of the living entity and the quality of the environment. The organisms must distribute themselves regionally in conformity with their own genotypical nature which is adapted to certain environmental conditions. But in the geographical distribution of the various species which thus comes about, there is not stagnation but change. And this change has its cause in the same two factors which we have mentioned above. The germ plasm may change; we call such changes mutations. Through these the organism becomes adapted ("pre-adapted") to new environmental conditions and is able to take possession of new regions. And the environment may change in various ways and thus give formerly useless mutations a "place in the sun". On the other hand changes in the germ plasm and environment may become unfavourable to the species and lead in time to its extinction. As far back as we have been able to trace life into ancient times, each geological period has shown examples in plenty of changes both in the organisms and in inanimate nature. Biologists have no difficulty in regarding time as a sort of fourth "dimension" in the whole of nature.

Throughout the phylogenetic evolution species, genera, families and so on and faunas have appeared, changed and disappeared. By the events in inanimate nature mountains and the deeps of the sea,

147. Ekman, S. (1940) Begrundung einer statischen Methode in der regionalen Tiergeograpie. *Nova Acta Reg. Soc. Sci. Upsaliensis*, 12:2.

ocean currents and climatic zones have appeared, changed and disappeared and as a result of interactions of infinite complexity between animate and inanimate nature the present biogeographical conditions have emerged in the course of the ages. Time, which is in reality nothing more than the succession of events, that is historical happenings, is a factor of profound importance for all manifestations of life. In other words: biogeography cannot confine itself simply to describing the occurrence of living forms, arranging them regionally, investigating the ecological causes of distribution. It must also proceed historically.

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From *An Introduction to Historical Plant Geography*

Evgenii Vladimirovitch Wulff

Chapter X

HISTORICAL CAUSES FOR THE PRESENT STRUCTURE OF AREAS AND THE COMPOSITION OF FLORAS

From the preceding chapters it is clear that in many cases the structure of the areas of species and the composition of floras cannot be explained by existing factors. The present distribution of any given species is a reflection of the geological revolutions and climatic changes that have occurred on our globe during the entire period of existence of that species. An elucidation of these great changes in the surface of our planet is the task of historical geology and paleogeography, a task as yet far from fulfillment. Consequently, the elucidation of the history of areas, the most difficult task of biogeography, likewise falls far short of achievement. In the present chapter we can, therefore, do no more than examine the chief theories that have been advanced and point out which give the most plausible and satisfactory explanation of the knotty problems of historical plant geography.

From very ancient times—at first without adequate foundation and later, with the development of geology and biogeography, on the basis of numerous data—the conviction has been held that the distribution of lands and seas was not always the same as now. For, if it had been, a considerable number of facts, both of a geological and biogeographical nature, would be inexplicable. The sedimentary character of the rocks covering extensive territories on the continents and the finding in these rocks of fossil marine animals testify to the fact that at one time seas covered these parts of the continents. That many islands formerly constituted a part of the mainland is shown by the geological structure of these islands, by their fossil and extant fauna and flora, and by the finding of submerged trees in various straits and channels, *e.g.*, in the English Channel. Furthermore, the outermost edges of continents and islands do not necessarily coincide with their shore lines, as their outer margins often lie submerged under so-called "shelf seas". The latter differ in extent, but their boundaries may be ascertained with considerable precision. The determination of these boundaries gives certain clues to the changes that have taken place in the distribution of lands and seas on the globe and on the probable existence in former times of connections between bodies of land now separated by the sea. Biogeographical data, in many cases, indicate that these changes occurred at a comparatively recent date.

1. *Theory of Land Bridges.*—We have already seen that a considerable number of cases of discontinuous areas of plants (and these might be supplemented by an equal number of instances of similarly distributed animals) cannot be regarded as accidental and require explanation. Often there seems to be only one possible explanation, *viz.*, that there formerly existed some sort of connection between the isolated habitats and that the now discontinuous areas were formerly continuous. Hence, many investigators have assumed that at one time