RECTIGRADATIONS AND ALLOMETRONS IN RELATION TO
THE CONCEPTIONS OF THE "MUTATIONS OF WAAGEN,"
OF SPECIES, GENERA, AND PHYLA ¹

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CONTENTS

	Page
General discussion.....	411
Discussion of the illustrative diagrams.....	413
Space, geographic divergence, and evolution.....	414
Geographic distribution.....	416

GENERAL DISCUSSION

The new problem raised in this contribution is that of the comparison of a geologic ascending evolutionary series in time, like that of the titanotheres, with a contemporaneous geographic series of species, subspecies, and varieties which may be grouped within a single genus: In what respects do the characters observed in a genus ascending and developing in geologic time resemble or differ from the characters observed in a genus distributed in geographic space?

The superb materials assembled by Osborn with the cooperation of William K. Gregory for the study of the titanotheres enable us to determine with precision that in a *time series* there are two kinds of characters in the hard parts of mammals, namely, *allometrons*, or changes of proportion, and *rectigradations*, or the appearances of absolutely new characters. For example, a new cusp or a new horn rudiment is regarded as a rectigradation in its initial stage; but when it takes on profound changes of proportion in the course of evolution these changes are known as allometrons. These characters appear to evolve under a different combination of causes. The accumulation of allometrons and rectigradations marks the steps from "species" to "species" and the minute continuous

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transition stages between species which correspond to the "Mutations of Waagen."

TABLE I.—Showing the space, or geographic differences in mammals observed by the zoologist, and the time, or geologic differences observed by the paleontologist. A, central or stem form. A-C, A₁-D₁, geographic "species." A-F, geologic species.

In a geographic, or *space series*, on the other hand, as in the case of genera of very wide geographic range, we observe both color changes, changes of proportion, or *allometrons*, and in rare instances new structures which appear to resemble *rectigradations*. These geographic sub-

species and varieties have been studied extensively by Merriam, Miller, Osgood, and other mammalogists, but the characters which have been used to distinguish them have not yet been analyzed in comparison with the characters which are employed by paleontologists to distinguish the ascending geologic mutations and species.

DISCUSSION OF THE ILLUSTRATIVE DIAGRAMS

The accompanying diagrams present in graphic form this future problem for the cooperation of the zoologist and paleontologist who have made observations independently hitherto without comparison of their separate results. The very circumstance that these facts have been garnered independently by workers in two fields of observation, with no purpose but the *close definition and distinction of nearly related forms*, renders all the more valuable any results which may be obtained in the future. In other words, the facts have been garnered both in zoology and vertebrate paleontology without that bias or preconceived theory which often influences us to observe some facts rather than others.

The problem of this comparison between zoologic and paleontologic series is complicated by the fact that all zoologic series which are of wide geographic range must necessarily be widely separated *in time* as well as *in space*. For example, the genus *Peromyscus* as studied by Osgood (1909) presents a continuous series of transitions in color and form from the types which we observe on the Isthmus of Tehuantepec to those we observe in Alaska. In the northerly region we find a larger animal, with a relatively longer tail and a skull which may be somewhat longer or more dolichocephalic. The genus *Perognathus* offers better examples of skull change in connection with geographic distribution, for instance, in the form of the interparietal bone. The wide distribution of *Peromyscus* may have taken place from some common center during post-Glacial time, that is, during the last 20,000 years. In this period there has been both a *space evolution* and a *time evolution*, the latter being comparable to that which would be observed in a geologic series. This principle is clearly brought out in the accompanying diagram, in which A represents the stem or central form from which the geographic races have been given off, which in course of time, undergoing an evolution in time of from 5,000 to 40,000 years, diverge from the parent form (A) precisely like the geologic or time series. Forty thousand years may have elapsed since a geographic species or subspecies separated off from the parent form. Even in geologic estimates 40,000 years is an appreciable interval, in which new allometrons may arise and new rectigradations may appear.

TABLE II.—*Contrast between space evolution (geographic) and time evolution (geologic) from a central or stem form A*

A I-VI is an actually recorded series of ascending "Mutations of Waagen" and "species," assembled in the "genus" *Menodus*.

A-D and A¹-D¹ are hypothetical geographic varieties, *et cetera*, of *Menodus*, which probably existed in Lower Oligocene times for the "genus" is now known to have ranged geographically from South Dakota to the vicinity of Prag, Bohemia (*Menodus bohemicus*).

SPACE, GEOGRAPHIC DIVERGENCE, AND EVOLUTION

Somatic changes rapid and conspicuous; germinal changes gradual

Environmental (ecologic) and ontogenetic (habitudinal) influences producing divergent somatic effects on animals of similar ancestral stock, "environ-

mental or ontogenetic species," "sub-species," "races," "varieties," distinguished by different coloring, habits, proportions ("allometrons"), and perhaps by "rectigradations."

It follows that to institute a true comparison between a geographic series and a geologic series precisely the *same methods of observation* should be employed. Direct measurements of length and breadth should be recorded from which *indices* (proportions of single structures like the skull) and *ratios* (proportions between different parts like the upper and lower segments of limbs) should be established.

It is already known that allometrons, or changes of proportion, in every part distinguish the various geographic species and subspecies of *Ursus*, for example, as studied by Merriam, the changes technically known as dolichocephaly, brachycephaly, dolichopy (or elongation of the face), brachyopy (abbreviation of the face), brachypody (abbreviation of the feet), dolichopody (elongation of the feet), brachymely (abbreviation of the limbs), dolichomely (elongation of the limbs), occur in zoologic series *in their incipient stages* exactly as they occur in paleontologic series. The only distinction is that in paleontologic series they may be followed through vastly greater periods of time in all the stages from incipency to the various climaxes.

For example, the ten phyla of titanotheres described in the preceding contribution are distinguished by progressive changes of proportion in different directions. Thus one phylum is progressively brachycephalic until it reaches an extreme in which the breadth of the head is as great as the length; another phylum is progressively dolichocephalic until the head reaches a long, attenuated form.

TABLE III.—Showing that geographic or space distribution and geologic or time distribution may take place coincidently from a central stem form A during such an epoch as the post-Glacial.

GEOGRAPHIC DISTRIBUTION

Whether the causes of these changes are to be sought in heredity or ontogeny or environment or selection, or in the interactions of these four coefficients of evolution, is a problem which remains obscure to the paleontologist working in paleontology alone; but it may be illuminated by the combined observations of the paleontologist and the zoologist in cooperation, as proposed in this paper. The zoologist has already demonstrated that there is direct relation between certain types of coloration and environment, as well as between certain habitats and harmonic increase or decrease in size; it remains to be determined, chiefly by the zoologist, whether certain environments induce uniformly similar allometrons. Our present evidence indicates that this is not the case. Anthropologists have failed, for example, to establish any definite relation between environment and human head form. Again, the selection-value of allometrons, or changes of proportion, is obvious in certain cases; but not at all apparent in others. Gerritt S. Miller also fails to observe any direct relation between environment and head proportion, although an indirect relation may arise in connection with differences of food and feeding habits in different environments.

The author has already (May, 1914) been promised the cooperation of a number of eminent mammalogists in a comparison of zoologic² with paleontologic data which may be fruitful of important results.

² Gerritt S. Miller (May, 1914) observes that there are abundant illustrations of the direct action of environment on color in mammals, but that as to proportions, size, and cranial characters the case is quite different. In other words, there are plenty of instances of color changes of different character affecting many different members of a fauna in the same way, as when we pass from a wet to a dry climate or from a low to a high altitude, but there do not appear to be any parallel set of changes in proportions, size, or structure.