

MIGRATION AND SHIFTING OF DEVONIAN FAUNAS¹

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(Presented in abstract before the Paleontological Society Dec. 31, 1909)

CONTENTS

	Page
The hypotheses of recurrence and shifting of faunas stated.....	285
Facts on which the hypotheses rest.....	286
Catskill sedimentation	286
Reversal of order in succession of faunas.....	286
Recurrent Hamilton fauna	287
Alternate appearance of diverse fossiliferous zones.....	287
Limited range of recurrent species.....	288
Interpretation of the facts.....	289
Shifting of faunas.....	289
Lithologic changes not sufficient to account for differences in faunas..	289
Difference in ocean waters presumed.....	289
Migration of species and shifting of faunas contrasted.....	290
Changed environment cause of both migration and shifting.....	291
Close adjustment of species of a shifting fauna.....	291
Evidence of migration.....	291
Recurrence	292
Theoretical problems involved.....	292
Evidence of faunal continuity.....	292
Rare and dominant species.....	292
Magna faunas and local special faunas.....	293
Fixed and fluctuating characters.....	293
Difficulties in establishing evidence of strict contemporaneity.....	294

THE HYPOTHESES OF RECURRENCE AND SHIFTING FAUNAS STATED

In 1881 I presented before the American Association for the Advancement of Science the first definite announcement of the hypothesis of recurrent faunas, applying it to the fauna of the Marcellus, Genesee, and Ithaca black shales of new York, which I then conceived to be represented

¹ Manuscript received by the Secretary of the Geological Society April 23, 1910.

by the continuous fauna of the black shales of Ohio, Indiana, Kentucky, and Tennessee; and also, in the same paper, the hypothesis of shifting of faunas was applied to the Hamilton and Chemung faunas of central New York.² Since that time a large amount of evidence has been accumulated confirming these hypotheses. These hypotheses are intimately correlated. Recurrence or the departure of a fauna, its replacement by another, and its final reappearance in the same section at a higher level become the facts on which the hypothesis of shifting of the faunas is based; and the assumption of continuance and shifting of a fauna without losing its characteristics appears to be the only satisfactory explanation of its recurrence.

FACTS ON WHICH THE HYPOTHESES REST

The following facts explained by these hypotheses are among the more important which have come to light in the course of my studies.

CATSKILL SEDIMENTATION

This was shown to be thicker and to start lower down in the geological column in eastern New York than in middle and western New York. In eastern New York it began while the Hamilton marine fauna was still present and cut it off, bringing in estuarian conditions with a brackish water and land fauna and flora. In central New York no Catskill sedimentation is present until after the arrival of the Chemung fauna, and in western New York no trace of the Catskill type of sediments appears till after the close of the Devonian. These facts are direct evidence of shifting of the environmental conditions of the edge of the continent westward as the deposits of the middle and upper Devonian were being laid down. With this shifting westward of the off-shore conditions of the sea there went on a corresponding shifting of several faunas that were adjusted to each phase of those conditions.³

REVERSAL OF ORDER IN SUCCESSION OF FAUNAS

The appearance of the dominant species of the general fauna in reversed order of succession at the close of a fossiliferous zone.

The cases of *Spirifer laevis* in the Ithaca zone and of the frequent appearance of *Leiorhynchus* at the opening and close of a fossiliferous zone were among the earliest observed facts suggesting an actual shifting

² Proceedings of the American Association for the Advancement of Science, vol. xxx, p. 186, etc.

³ "On the classification of the upper Devonian." Proceedings of the American Association for the Advancement of Science, vol. xxxiv, 1885, p. 222.

of the body of a fauna entering the area in one order of succession and departing in the reverse order.

In the Ithaca section there occurs at the base of the fossiliferous zone of the Ithaca member a bed containing abundance of *Spirifer* (*Reticularia*) *lævis*. The discovery of the same species at the top of the fossiliferous zone, as the normal Ithaca fauna become sparse, gave the first suggestion that the faunas were moving or shifting, the *Reticularia* zone marking the first trace of the fauna to enter and the last to leave the area. Confirmatory evidence was found in the order of succession of the dominant species of the Ithaca fauna. These facts were reported in 1883.⁴

The study of the mode of occurrence of *Leiorhynchus* still further drew attention to the definite order in which a series of species came in and went out of any given area. The species of the genus were generally found abundantly at the base or at the top of fossiliferous zones rich in brachiopods, in the midst of which *Leiorhynchus* was rare.⁵

RECURRENT HAMILTON FAUNA

The occurrence in a single or few strata of several representatives of an earlier fauna long after the formation to which they are normal has ceased.

Slight traces of this fact were observed in the first survey of the Devonian section passing through Ithaca,⁶ and the fauna numbered 14 N (page 15) was called a "recurrent Hamilton fauna" because of the appearance there of such species as *Spirifer fimbriata*, *Sp. augusta*, *Pleurotomaria capillaria*, and others; and higher up, in the midst of the Chemung section, at Chemung narrows, *Tropidoleptus carinatus* and *Cypri-cardella bellistriata*, *Phacops rana* and *Dalmanites calliteles* were found.

The discovery of such traces of an earlier fauna led to further search, and as the evidence accumulated an elaboration and definite formulation of the theory of recurrence of faunas was made, which has been set forth in several papers, and is illustrated in detail in the folio of the Watkins Glen-Catatonk quadrangles, constituting folio number 169 of the U. S. Geological Survey.

ALTERNATE APPEARANCE OF DIVERSE FOSSILIFEROUS ZONES

The facts there brought out are substantially as follows:

There are exhibited in the sections mapped for the quadrangles *two*

⁴ Bulletin 3, U. S. Geological Survey, p. 20, and Proceedings of the American Association for the Advancement of Science, vol. xxxiv, 1885, p. 222, etc.

⁵ See Bulletin 3, U. S. Geological Survey, 1883, pp. 16 and 17,

⁶ Reported in 1883, Bulletin 3, U. S. Geological Survey,

series of fossiliferous zones, the separate zones of the two series alternating in succession.

The zones of one series *dominate* the western sections of the area, and thus thin out or disappear on tracing them eastward. The zones of the second series dominate the eastern sections, and particularly the whole eastern New York sections, but thin out westward, and in some cases are entirely wanting in sections west of the Watkins Glen quadrangle.

The first set of faunal zones includes the faunas of the Genesee shale, the Portage formation, and the several divisions of the Chemung formation.

The second set of zones includes the Hamilton fauna, proper and recurrent representatives of that fauna, which I have named the *Paracyclas lirata* zone; the *Spirifer mesistrialis* zone; the *Leiorhynchus globuliformis*, or Kattel Hill zone (representing the typical Ithaca group of Hall at its typical sections at Ithaca); and the first, second, and third recurrent *Tropidoleptus* faunas, which I have called the Van Etten, the Owego, and the Swartwood *Tropidoleptus* zones.

All of these several fossiliferous zones of the second set become decidedly thin on passing westward across the region.

The Ithaca fauna is occasionally detected west of the Watkins Glen quadrangle, but is confined to less than 100 feet at Watkins, is recognized for 300 feet at Ithaca, and ranges through at least 600 feet along Tioughnioga River.

Only a slight trace of the *Paracyclas* zone is seen as far west as Ithaca, but is well expressed in the sections on the east side of the area.

The Van Etten, Owego, and Swartwood *Tropidoleptus* zones appear in thin tongues of strata as far west as the Waverly quadrangle and are seen in occasional traces as far west as the Elmira quadrangle, and when followed eastward appear to blend together as a modified Hamilton fauna, sparsely appearing in the strata up to the arrival of the Catskill type of sedimentation.

LIMITED RANGE OF RECURRENT SPECIES

Where the Hamilton recurrent zones are seen in sharpest expression the recurrent species range through only a foot or a few feet of strata, hold in abundance four or five characteristic Hamilton species, such as *Tropidoleptus carinatus*, *Cypricardella bellistriata*, *Rhipidomella vanuxemi*, *Spirifer marcyi* and *Delthyris mesicostalis*, cf. *D. Consobrinus*, and others, and the Owego and Swartwood zones appear in the midst of a characteristic Chemung fauna present both above and below each recurrent zone.

In the Owego recurrent zone both *Phacops rana* and *Dalmanites calliteles* occur.

The Van Etten recurrent zone lies entirely below the range of *Spirifer disjunctus* and other associated species of the Chemung formation.

On following the sections eastward from the Waverly quadrangle the species of the Chemung fauna become scarce, and east of the Chenango River very few species of the typical Chemung fauna have been detected, although they are still abundant in the Chemung rocks to the southeastward and southward across Pennsylvania, Maryland, and Virginia.

INTERPRETATION OF THE FACTS

SHIFTING OF FAUNAS

These facts have been interpreted as evidence not only of a general shifting of faunas coincident with a rising of the land along the eastern edge of the present continent, but of oscillation of conditions and alternate occupation of the area by two sets of faunas coming from opposite directions and temporarily living in abundance in the area of central New York.

LITHOLOGIC CHANGES NOT SUFFICIENT TO ACCOUNT FOR DIFFERENCES IN FAUNAS

The lithologic changes in the sediments containing the different faunas are not sufficient to account for the change in fauna. In quite a number of sections there is no appreciable difference in lithologic constitution between the strata which for 100 feet thickness have been filled with characteristic Chemung species and the immediately following thin zone of a foot or two, containing scarcely a trace of the Chemung species, but holding in great number species which if found by themselves would be undisputed evidence of the Hamilton formation.

DIFFERENCE IN OCEAN WATERS PRESUMED

It becomes necessary therefore to suppose that the controlling cause determining the presence of one or other fauna is not the character of the bottom on which the sediments which preserved the fauna were laid. We are thus led to conclude that the character of the ocean water has determined the shifting or migration of the faunas. The conditions to which the faunas were adjusted were evidently those of depth, salinity, or temperature of the waters in which the species lived; and their change of habitation was occasioned by change in the direction, path, or extent of flow of the oceanic currents.

This leads us to consider the general principles of migration, and in particular those which affect marine organisms.

MIGRATION OF SPECIES AND SHIFTING OF FAUNAS CONTRASTED

Migration as commonly applied in natural history means the movement of large numbers of the same species from one place to another in a general definite direction at more or less regular periodic times. So birds migrate northward with the advance of warm weather; some fish migrate from sea to rivers in breeding seasons; pigeons fly eastward or westward in great flocks; grasshoppers invade a rich country, devouring the vegetation in their path, or lemming migrate in great hordes from mountain to lowlands.

The term in these cases has to do with movements of one kind of animal in relation to the comparatively fixed range of feeding ground for the remainder of the fauna inhabiting the areas concerned. The term is rarely applied to the slower movement of the whole body of animals of a fauna, coincident with great changes of climate such as the advance of the glacial cover over the northern parts of Europe or America produced during the Glacial age, or the advance of an Asiatic fauna across the Bering Straits and down the west coast of North America at some Pleistocene time, when an ice-bridge furnished means of communication by land from one continent to the other. Perhaps there is no impropriety in extending the application of the term migration to these latter cases in which the whole fauna and flora of a region are affected instead of a single or a few species, and in which the change of position of habitat is slow and spread over a great period of time instead of being coincident with annual change of seasons. The term may equally well be applied to movements in the seas and movements on the lands.

There is, however, one reason for choosing a separate name for the movements of the latter kind to distinguish them from typical migration: In the first class of cases the migration is voluntary and is performed by those organisms which have the power of more or less rapid locomotion. They may be said to do the migrating themselves. In the second case the movements are involuntary and the movement is forced on all the living organisms of the region. The change in position may be supposed to take place by the contraction on one side of an area of the conditions of possible existence for the species and the extension on the other side of favorable conditions of environment. The movements extend over many generations of life, so that relatively sedentary species may gradually adjust their *locus habitans* in the given direction of mo-

tion. To this latter process of migration I have been accustomed to apply the term "shifting of faunas."

Migration of species is in its typical sense an expression of the ability of some organisms to appreciate slight favorable changes in the conditions of environment and to take advantage of the better conditions during the lifetime of an individual. Shifting of faunas is an expression of the felt necessity, for the perpetuation of the race, of certain conditions of environment, resulting in the dying out of the whole fauna in the areas from which the favorable conditions have been removed and the spread of the fauna into new areas into which the favorable conditions have been shifted.

Shifting of faunas is an expression of the inability of any species of the fauna to survive under the changed conditions of environment which have overwhelmed them in their original habitat, but of an ability on the part of all those which migrate to follow the favorable conditions as they shift from one area to another.

CHANGED ENVIRONMENT CAUSE OF BOTH MIGRATION AND SHIFTING

In both typical migration of species and shifting of faunas, change in the environmental conditions of life constitutes the stimulus inducing change of habitat on the part of the organisms, and the movement of the organisms is a direct response to the stimulus. Those organisms in the first case which migrate show their greater vitality, compared with their neighbors who stay at home; while those who stay at home show the greater power of endurance and of organic adjustment to a wider range of environmental conditions than do those which migrate.

CLOSE ADJUSTMENT OF SPECIES OF A SHIFTING FAUNA

In the case of the shifting fauna, those species which endure without change of characters exhibit an acquired closeness of adjustment to some particular combination of environmental conditions which they are forced to follow or die and suffer annihilation. The evidence of their endurance is indicated by their return and reoccupation of the same area at a later geological stage when, by their reappearance, the original condition of environment is shown to have recurred.

EVIDENCE OF MIGRATION

In the case of living organisms evidence of migration is found in the actual presence of the species at one time in a region at a considerable

distance from its ordinary *locus habitans*; and in some cases the species may be seen in the process of migration, as, for instance, the temporary alighting, in fatigued condition, of flocks of northern land birds on Bermuda Island on their migration southward.

In the case of fossil species the shifting of a fauna is recognized by the presence in a stratum of rocks of a number of species representing an earlier fauna surrounded by a different and, dominantly, later set of species.

RECURRENCE

The fauna is then said to *recur*, and it is the recurrence of the fauna which forms the basis for the inference that the fauna has shifted its *locus habitans* during the period of time represented by the sedimentary deposits separating the formation in which the fauna is dominant from the zone in the higher formation in which the recurrent species are found.

THEORETICAL PROBLEMS INVOLVED

This hypothesis of shifting of place and recurrence in time of a fauna involves certain conceptions as to the nature of species and the laws of evolution which it is important to consider.

EVIDENCE OF FAUNAL CONTINUITY

To establish evidence of motion in migration, as in any other kind of motion, it is all important to know that the body or bodies to which the motion is ascribed is continuously the same.

In the Devonian case the moving body is a fauna. Not only is it necessary to establish identity of the species in the recurrent zones with those of the initial zones, but it is essential to show that the faunas as a whole are the same. To put this in another mode of statement, we must establish the fact that not only the individual species have retained their specific characters, but the further fact that the equilibrium of adjustment to each other in the faunal community has not been changed, in order to prove that a supposed recurrent fauna is actually the direct successor of a fauna represented in the rocks at a lower horizon.

RARE AND DOMINANT SPECIES

This has led to the distinction between rare and dominant species. Only as the comparative frequency of the species in the faunal combination is maintained can we be sure that we are not considering an acci-

mentally accumulated sample of a general fauna instead of the successive appearance of a special fauna.

The presence of an occasional associated species belonging normally to the fauna of the formation in which the recurrent zone appears is not antagonistic to the hypothesis, because the hypothesis proposes an invading of the territory already occupied by a normal fauna; and in case the currents or other causes which brought about the shifting of the fauna were not so completely different as to annihilate all evidence of the fauna previously occupying the ground, some few species might be supposed to hold over. Hence it is only necessary to find an abrupt change of the majority of species to make the induction that the faunas have shifted their habitats.

MAGNA FAUNAS AND LOCAL SPECIAL FAUNAS

The theory involves the further conception of grand general faunas or magna-faunas which have their center of habitat and distribution in permanent oceanic basins, as distinguished from the local, special and (in geological strata) temporarily expressed faunas, such as we are accustomed to associate with individual geologic formations.

In the case before us two such magna faunas are in evidence, one of which in its dominant characteristics is traced westward into Iowa, Idaho, and Arizona and up the Mackenzie River valley to the north, and across the polar regions to Russia and northern Europe. The other is traced eastward and southward into central and southern Europe, and also appears dominantly in South America.

In a case of recurrence in which there has been continuous sedimentation it is practically impossible to distribute all the species according to their source of origin. I have found it possible, however, to distinguish a few species as undoubtedly derived from a source different from that of the prevailing fauna characterizing the beds both below and above the recurrent zones.

FIXED AND FLUCTUATING CHARACTERS

It is only by close examination and comparison of the fossils themselves that identity of species or identity of faunas can be established.

The fixed characters are not only those characters by which one species is distinguished from another, but they include others of generic, ordinal, and even class rank, which may be of immense age in the race and mark no special narrow stage of its history.

It is a question of interpretation whether each particular phase of expression of fluctuating characters is a matter of time or of environment.

I have reached the conclusion that it is those species whose characters have the greater degree of normal and persistent fluctuation which migrate and follow the shifting conditions of environment, and their life period is correspondingly longer.

On the other hand, species whose plasticity of characters is narrow are more closely adjusted to their environment, are local in their range of habitat, and are temporary in their geologic life period.

Interpreting the facts on this basis, it is the phases of continuously fluctuating characters in species of wide geographic distribution and of long geologic range which furnish the most satisfactory evidence of temporary stages in the life history of faunas.

DIFFICULTIES IN ESTABLISHING EVIDENCE OF STRICT CONTEMPORANEITY

Another question of interpretation arises when we attempt to reconstruct the physical condition of the environment at successive stages of time.

In a single vertical section we have positive evidence of succession in time. If we were sure that no recurrence of the same fauna could take place, we could correlate two vertical sections strictly upon the fauna contained in the strata—on the hypothesis that the single fauna existed but once, and when it ceased in a given section its whole life period had been expressed. But the facts show us that this is not the case in nature. In geological times, as in the present, we know that many distinct faunas are living on the face of the earth at the same time, even for very similar conditions of environment. It becomes, therefore, a very complex matter to establish the fact of contemporaneity or to correlate two sections in which the order of faunas and the character of the sediments differ, which is generally the case for any two sections separated by 50 miles from each other, although on stratigraphic evidence they may be properly interpreted as covering the same interval of time.