

upon which this law was based, that of E. Schütz³ in 1885 and the confirmatory data of Borissov⁴ in 1891 and J. Schütz⁵ in 1900 shows merely that in the presence of varying concentrations of pepsin, the *amounts of protein digested at a given time* (e.g., 16 hours in the work of E. Schütz) are proportional to the square root of the enzyme concentration. In so far as the Schütz-Borissov formulation limits itself to the summary of these particular results or similar results for other enzymes, it is correct, though naturally quite limited in its significance.

That formulation, however, of the Schütz-Borissov or of similar data which aim at wider significance by stating that the *velocity of reaction* is proportional to the square root of the enzyme concentration is based on an incorrect use of the term "velocity of reaction." This error is easily revealed by mathematical treatment of the kinetics of the reaction involved, and it may be shown that E. Schütz's own data support the general rule, established so widely for other enzymes, that the reaction velocity is directly proportional to the first power of the concentration of enzyme.

E. Schütz determined the extent of action at only one point, 16 hours, submitting no data on the course of the reaction. Arrhenius⁶ in 1908, as well as others since then, noted that under most conditions the amount of protein digested at a given concentration of pepsin preparation could be fairly well expressed as being proportional to the square root of the time, for about the first 50 per cent. of the hydrolysis.

The course of the action may then be expressed at two levels of enzyme concentration, A and B, in terms of reaction constants, as follows:

$$k_A = \frac{1}{t} \cdot x^2$$

and

$$k_B = \frac{1}{t} \cdot x^2$$

where x is the amount of protein digested at time t . The ratio of the reaction constants is, for a given value of t as, for example, 16 hours in the experiments of E. Schütz,

$$\frac{k_A}{k_B} = \frac{x_A^2}{x_B^2}$$

In other words, as the enzyme concentration is varied, the ratios of the reaction constants, which are a proper measure of the velocity of the reaction, are equal not

to the ratios of the amounts changed in a given time, but to the ratios of the squares of these amounts. According to E. Schütz's own data, the amounts changed in a given time are proportional to the square root of the enzyme concentration,

$$\frac{x_A}{x_B} = \frac{\sqrt{E_A}}{\sqrt{E_B}},$$

or

$$\frac{x_A^2}{x_B^2} = \frac{E_A}{E_B}.$$

Since, as shown above,

$$\frac{x_A^2}{x_B^2} = \frac{k_A}{k_B},$$

then

$$\frac{k_A}{k_B} = \frac{E_A}{E_B},$$

or the reaction velocity is directly proportional to the concentration of enzyme, not to the square root thereof.

When the reciprocal of the time required to reach a given stage in the enzymic reaction is used as a measure of reaction velocity (and this is a more proper measure than the amount changed in a given time, although it also has limitations) there may be instances in which the Schütz-Borissov law seems to be approximated or even followed. But such simulation appears to be due, at high concentrations of enzyme, to the presence, as impurities in the enzyme preparation, of proteolytic products which apparently combine with the enzyme to form enzymically inactive compounds.^{7,8}

There would appear to exist, therefore, no substantial data to contravene the general rule that the velocity of reaction is directly proportional to the concentration of enzyme, within rather wide range of the latter. Data indicating such contravention must be evaluated with respect to (a) the measure of reaction velocity used and (b) the possible presence of accompanying substances, impurities or reaction products which affect the activity differently at different enzyme concentrations.

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RELIC FLORA IN RELATION TO GLACIATION IN THE KEWEENAW PENINSULA OF MICHIGAN

In a paper entitled "Critical Plants of the Upper Great Lakes Region of Ontario and Michigan," which

³ E. Schütz, *Zeits. physiol. Chem.*, 9: 577, 1885.

⁴ Borissov, Inaugural Dissertation, St. Petersburg, 1891, quoted by J. Schütz.

⁵ J. Schütz, *Zeits. physiol. Chem.*, 30: 1, 1900.

⁶ S. Arrhenius, *Medd. Kong. Vetsakad. Nobelinst.*, 1908, 1.

⁷ J. Northrop, *Jour. Gen. Physiol.*, 2: 471, 1920.

⁸ O. Bodansky, *Jour. Biol. Chem.*, 114: 273, 115: 101, 1936.

appeared in Vol. 37 of *Rhodora* for 1935, Dr. M. L. Fernald has introduced an attempt to substantiate a view that certain portions of the Keweenaw peninsula of northern Michigan escaped glaciation during the Wisconsin stage of the Pleistocene. His contentions are based essentially upon botanical evidence as related to the existence there of "a great assemblage of remotely isolated relic species and isolated endemics" (p. 205), representatives of which are found only in areas widely removed from this center. The criteria which he employs in an effort to discount the possibilities of a Wisconsin invasion of the ice sheet in the region of "West Bluff" (p. 204), for instance, are wholly inadequate to prove his contention. The glacial facts at hand were either grossly overlooked or deemed too unimportant to be given consideration in the problem. With these points in mind the writer made a special trip into the Keweenaw peninsula for the purpose of ascertaining the status of the area in so far as geological evidences for glaciation are concerned. On the basis of this field investigation, I am compelled to take issue with Dr. Fernald in his hypothesis for a "driftless" condition in the Keweenaw region. The evidences for glaciation, even in the higher levels of the bluffs, are so obvious that it is difficult to understand how they could have been missed by him. If Dr. Fernald had taken pains to carefully scrutinize the composition of the terrane in the north slope of West Bluff, he would undoubtedly have noted that the rock pavement is mantled to the very summit with a thin veneer of glacial till. The drift cover of boulder clay contains numerous erratics such as granite, diabase, diorite and greenstone; rocks which are foreign to the local area.

In a recently opened road cut about 140 feet southeast of the U. S. Geological Survey bench mark, which marks the highest point of the bluff, the glacial drift had been scraped off to expose a narrow strip of bed rock for a distance of 50 or 60 feet. The conglomerate, which forms the pavement over which the ice sheet moved, carries numerous glacial striae and scratches which bear generally S.80°W. So powerful was the attack of the ice in the area that the striated cobbles and pebbles which comprise the conglomerate were planed off sharply. The striations and scratches on bed rock were traceable to within five feet of the summit level of the bluff. From this elevation to the crest, the rock pavement is masked by a mantle of boulder clay which was left by the wasting ice in its retreat. Glacial evidences in the form of bouldery till, striations on rock floor and ice-planed cobbles within the pavement conglomerate certainly can not be utterly disregarded, in consideration of the problem concerning glaciation. On page 204 of his paper, Dr. Fernald

refers to the "rotted" condition of the material comprising "West Bluff" and seems to make quite an issue of the fact that the atmosphere was filled with "clouds of wind-blown sand and dust of purely local origin." That the material is of local origin is not demonstrated and, so far as I can reason, there is no particular point in emphasizing facts concerning aeolian translocation in the light of attempting to prove either the presence or absence of glacial deposits in a given locality.

On page 205, Fernald states that his interpretation is supported by botanical evidence:

Keweenaw County has a greater assemblage of remotely isolated relic-species and isolated endemics than any other botanically explored region between Gaspé Cliffs and mountains and the Driftless Area of Wisconsin, Minnesota, Iowa and Illinois.

It is not my purpose to attempt to discredit Dr. Fernald's observations that the Keweenaw peninsula harbors a wide floral range whose counterparts on the continent are widely separated. I am thoroughly convinced, however, that criteria other than those set forth by him are necessary to clarify the problems related to the concentration of so-called relic-species in this locality. He then indicates the need for checking geological interpretations elsewhere on botanical evidence.

On page 217 of his report we find the following statements:

These observations on the Keweenaw Peninsula inevitably suggest that similar conditions will be found in other sections of the Upper Great Lakes area, especially where elevated and vertical escarpments and sharp bluffs stand high above the general level. So long as the botanist meekly accepts, without personally checking, the proposition that all the Upper Great Lakes region was completely under Wisconsin ice (and to a depth sometimes said to be 2000 feet) and then under the water of the Lakes he will fail to solve this striking phytogeographic problem. If he will visit the high bluffs and escarpments and himself *see* the conditions, he is likely to find that the bluffs of Keweenaw are not alone in lacking the abundant transported drift with which orthodox geology has blanketed them. He is likely to find that their crests and slopes have, instead, a rotted and angular crust or deeply weathered mantle *in situ*. It will then be demonstrated that there were in the Upper Great Lakes region *several driftless areas*, limited in extent but sufficient to have maintained colonies of the formerly wide-spread and somewhat generalized Tertiary flora, species which, in areas of active Wisconsin glaciation, were eliminated in favor of the younger and more aggressive series of plants.

I fear such checking elsewhere might have no better basis than on the Keweenaw peninsula. During the maximum extension of the Superior lobe, the Keweenaw and Chippewa tongues of ice became confluent upon the Keweenaw Peninsula and covered it com-

pletely. The ice of the Chippewa lobe extended to the southwestward for a distance of 150 miles beyond the Keweenaw Peninsula, and terminated there at an altitude some 300 feet above the level of West Bluff. It over-rode the Porcupine Mountains and other land areas near the Wisconsin line, where the relief is 500 and more feet higher than at West Bluff. To do this it must have been 1,000 feet or more above West Bluff for the surface of the ice sheet slopes downward toward its border.

If, as Fernald claims, the "relic-species" found in the Keweenaw Peninsula are hold-overs of a "formerly wide-spread and somewhat generalized Tertiary flora" (p. 217), then it is necessary to assume that the species in question not only survived the Wisconsin stage of glaciation but likewise the much longer and more wide-spread Illinoian stage as well. It is difficult for the glacialist to understand how the botanist gets his "relic flora" through an interval of 150,000 to 200,000 years of ice refrigeration, as represented by the Wisconsin and Illinoian stages, to say nothing of the much more protracted pre-Illinoian time, in the transition from the Tertiary to the present. Certainly the interval involving the wide-spread activities of pre-Wisconsin glaciation can not be neglected in the proper interpretation of the problem.

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"MIGRATION" AND "HOMING" OF PACIFIC SALMON¹

IN a recent issue of *SCIENCE*² Professor A. G. Huntsman stated that he was unable to find a single clear case of a salmon returning to its natal stream from a place in the sea away from the area influenced by the fresh water of its natal stream. He also assumed that salmon, when wandering in the sea beyond the gradient produced by their natal streams, become lost and may reach neighboring streams or travel farther to sea. Since Professor Huntsman has included the Pacific salmon of the genus *Oncorhynchus* in his category I would like to give evidence which shows that these salmon migrate to sea far beyond the influence of the gradients produced by their parent streams, mature and then return to their parent streams to spawn.

The Fraser River and its tributaries in British Columbia form one of the largest river systems on the Pacific coast of North America. This river system is noted for its high production of sockeye salmon (*O. nerka*) which form over 90 per cent. of the commercial catches of sockeyes in the Swiftsure Bank-Puget Sound-Fraser River region.³ There are also a number

of other streams of considerable size in this region, but only a few of them support populations of sockeye salmon, which in all form only a small fraction of the populations of the Fraser River system.

The majority of the Fraser River sockeyes migrate to and from the sea through the channels immediate to the river's mouth and the adjoining channel of the Strait of Juan de Fuca. The fresh waters of the Fraser River as well as those of all the streams in the Puget Sound area flow seaward through the Strait of Juan de Fuca. Since there are rapid tide movements in this strait these fresh waters become mixed shortly after they enter the strait. There is also a rapid mixing of the fresh waters with the salt water throughout the course of the strait so that no definite gradient is maintained. Hence if all the Fraser River sockeyes had to mature within an area in the sea influenced solely by the river's water or else become lost, they would all have to mature within the channels immediately adjoining the river's mouth. During the many years the salmon fisheries have been carried on in these channels as well as in the Strait of Juan de Fuca there is no record of the catch of partially mature sockeyes in these waters at any time in the year. In the years when salmon traps were operated in this region they were set weeks before the beginning of the spawning migration and yet no catches of partially mature sockeyes or adults were ever made at this time. In fact no adult salmon are ever caught within these waters except during the season of the spawning migration, which extends from May to October. During this period they are caught in the open sea on Swiftsure Bank as well as in the Strait of Juan de Fuca and the adjoining channels through which they migrate to the Fraser River.⁴ This is certainly sufficient evidence to show that the adult sockeyes which return to the river to spawn each season mature within the open sea far beyond the gradient produced by the fresh waters of the river.

Evidence which shows that the adult sockeyes which migrate into the Fraser River are native to it may be found in the studies of Dr. R. E. Foerster at Cultus Lake, British Columbia.⁵ This lake forms the headwaters of a tributary to the Fraser River. Thousands of young sockeye salmon from Cultus Lake have been marked by removing two or more of their fins. The adult salmon bearing these marks have been recovered by the fishery on Swiftsure Bank in the open sea, in the Strait of Juan de Fuca, in the waters in the immediate vicinity of the mouth of the Fraser River and in the river. Large numbers of adults bearing the marks have also been recovered at Cultus Lake. The

¹ Published by permission of the U. S. Commissioner of Fisheries.

² *SCIENCE*, 85: 313-314, 1937.

³ A complete description of this region and the commercial salmon fisheries it supports is given by G. A.

Rounsefell and G. B. Kelez, Special Rept. U. S. Bureau of Fisheries, 1935.

⁴ See H. O'Malley and W. H. Rich, Rept. U. S. Comm. of Fish., 1918, app. viii, 38 p.

⁵ R. E. Foerster, *Jour. Biol. Board Canada*, 3: 36, 1936.