THE ORIGIN OF THE SO-CALLED ATLANTIC ANIMALS AND PLANTS OF WESTERN NORWAY

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Contents

I. Introduction

The present essay is an attempt to account for the existence in western Norway of a complex association of plants and terrestrial animals not found elsewhere in Norway except as manifest peripheral radiations from a secondary center of distribution, which embraces the coast between Stavanger and Kristianssund.[1] These animals and plants display an unmistakable relation to a similar biota strongly developed more particularly in Scotland and northwestern Ireland, and it is here proposed to examine a little closer into this relation with a view to ascertain whether the connection is direct and genetic, or only indirect and due to parallel development. Because of the insufficiency of the material at hand as well as the unsatisfactory status of the scientific record, the inquiry only relates to a few selected forms and is primarily undertaken to serve as a foundation for a theory as to the origin of the biota which has received the somewhat unfortunate appellation "Atlantic" and to

[1] This stretch of the coast of Norway has no convenient distinctive name of its own. The Norwegian word "Vestenfjelds" is not exclusive enough, nor is "Vestlandet," both terms embracing much more of the country to the south of Stavanger as well as the interior fjord districts east to the watershed. It is often called "the northwestern fjord district," but "northwestern" is to some extent misleading and the term is cumbersome. In this paper when speaking of "west Norway" and "western Norway" I mean this coast strip between Buknfjord, in the south, and Trondhjemsfjord, in the north, or roughly between 59° and 63° north latitude.

incite further studies of the faunas and floras involved from the standpoint of this theory, in order that its merits or demerits may be thoroughly tested. The essay deals principally with biogeographic problems, but where it has been found necessary to introduce morphological matter in order to prove relationship, such questions are also discussed. Certain geological considerations which could not well be avoided have been set forth with due reserve, and in the most tentative manner.

In the course of his investigations the biogeographer when studying the dispersal of certain biota and their immigration into other regions is frequently facing facts which compel him to assume that the animals and plants have crossed territory now covered by the sea. The first question he then asks himself is whether there is any geological evidence in support of his theory. If not a geologist himself, he begins to study the geological literature. It has been my experience that whatever view I have taken, or from whatever side I have been viewing a question of this nature, I have always been able to find a geological theory and a geologist quotable in defence of my contention. Do I need a land connection in a certain place, there is always some geologist at hand willing to lift the ocean's bed thousands of fathoms even in comparatively recent times. If the views I have advanced concerning the biotic dispersal do not commend themselves to my fellow student, he may with equal confidence search the geological literature and sustain his opinion with quotations diametrically opposed. It is comparatively seldom that we are able to find paleontological evidence, and even then we are not always safe. Under these circumstances it seems to be the wisest course for the biogeographer to abide by the results to which he is led by his study of the present geographical distribution. If he can show then that his theories are not inconsistent with accepted principles and with the general outline of conservative geological opinion, he must remain satisfied. The details and the controversial points he may safely leave out, unless his own researches bear directly upon the latter.

The immigration of the biota of the Skandinavian peninsula after the great glacial period had destroyed most of the higher life previously existing there was comparatively early recognized by Swedish naturalists as having taken place along two different routes, viz., from the south across one or more Baltic land connections and a northeastern one over Finland and northwestern Russia. These two elements, the one descended from the biota of the central

European lowlands, the other composed of Russo-Siberian types, were easily recognized and accounted for. As the flora of Norway, especially the western part, became better known, a third element obtruded itself, namely, the one which Professor Axel Blytt called "the Atlantic group" of plants. These plants[1] he suggested had come from the "south and southwest," but from the context (*Forhandl. Vidensk. Selsk. Kristiania,* 1893, II, No. 5, p. 11) it is evident that he means the Danish peninsula, Jutland, the direction "south and southwest" being relative to his place of residence, Kristiania, not to western Norway.[2] Altogether the Norwegian botanists have been very vague in their statements regarding the origin of this flora, even Dr. Jens Holmboe, as late as 1903 (*Skr. Vidensk. Selsk. Kristiania,* 1903, I, No. 2, p. 201) speaks of the "*Ilex* flora" having "immigrated across the sea from the southwest," and of *Calluna vulgaris* he says (p. 213) that it is most reasonable to conclude that it has "immigrated across the sea," but by referring to the possibility of it crossing "an arm of the sea as broad as the Skagerak between Jutland and the south end of Norway" he plainly indicates the way he thinks it has come. The Swedish botanist, Dr. R. Sernander (*Skand. Veget. Spridningsbiol.,* 1901, pp. 414–416), is more direct, for he speaks (p. 416) of the *Ilex*-plants coming "clear across the Skagerak."[3] Most of the botanists, however, have held that the west Norwegian flora has wandered step by step and slowly from south Sweden to southeastern Norway and thence along the south coast past Lindesnæs and Stavanger to Kristianssund and the Trondhjemsfjord. As this question has been discussed voluminously and in great detail by the botanists, and as from the standpoint of the terrestrial animals it has received but little attention from the zoologists, the latter, as a rule and without questioning, have accepted the view of the majority of the botanists.

In February, 1901 (*Amer. Natural.,* XXXV, pp. 109–112) I had occasion to publish my theory that a certain number of animals

[1] For a definition of this group see further on p. 484.

[2] In his original paper on the immigration of the flora of Norway (*Nyt Mag. Naturvid.,* XXI, 1876, p. 349) Blytt hints at the possibility of the "Atlantic" flora having come to western Norway from a hypothetical "North Sea land," but because of the deep water along the west coast and of the Norway channel he thinks "it would be over bold to assume a land connection between our west coast and such a North Sea land."

[3] And even under this supposition he is surprised that they can have reached as far north as they have, "past Lindesnæs degree by degree of latitude up to Kristianssund" (p. 415).

such as the red deer, the tundra reindeer, the variable hare, the ermine, the Norwegian lemming, the ptarmigan, etc., invaded western Norway from Scotland on a land bridge across the North Sea. There was no opportunity then for going more into detail, but my reference to Sharff's map (Hist. Europ. Fauna, 1899, p. 156) roughly indicated this land connection as affecting only the *northern* portion of the North Sea. Since then I have occasionally referred to this theory in papers on the geographical distribution of the dippers (*Cinclus*),[1] and on the identity of the so-called Celtic horse (*Equus celticus*) with the west Norwegian pony.[2]

At the time of first making this theory public I also suggested that a certain element of the west Norwegian population "which holds the extreme west coast to almost the identical extent as the red deer" came to western Norway by "the North Sea bridge, either yet intact or only broken to the extent of furnishing stepping stones."[3]

This theory of mine respecting the origin of part of the west Norway fauna received considerable support from a theory bearing on the origin of the west Norwegian "Atlantic" flora propounded by Dr. Andreas M. Hansen in his remarkable book "Landnaam i Norge" (Kristiania, 1904). On pp. 293 to 298 he attempts to prove that these "Atlantic" plants which are now so characteristic of and mostly confined to the west Norwegian coast north of Stavanger are of "interglacial" age, that they came from the west, and that they survived the neoglacial stage[4] on a glacier-free border land skirting the western and northern coast of Norway.

Professor N. Wille has quite recently (1905) as will be noted more in detail further on (p. 486) accepted this theory for a portion of the so-called "Arctic" flora.

Hansen, however, does not mention the theory already published by me, which has so many points in common with his own. Alto-

[1] Smithson. Misc. Coll. (Quart. Issue), xlvii, pt. 4, 1905, p. 429.

[2] *Naturen* (Bergen), 1904, p. 166.

[3] Mr. Helliesen, curator of the museum in Stavanger, Norway, made a similar suggestion a few months later. In Stavanger Museums' Aarshefte for 1900 (published after May 9, 1901), pp. 57–60, he describes a paleolithic "kitchenmidden" from Jæderen, and concludes by saying: "From this oldest stone age people is probably descended the present brachycephalic race which is found especially in western Norway. It probably arrived in the country over the sea from Jutland or Scotland."

[4] By this term he understands the phase of the glaciations of the peninsula, which the Scandinavian glaciologists generally call the "second," or "last," glaciation. By "megaglacial stage" he designates their "first," or maximum, glaciation.

gether the question of a distinctly Scoto-Norwegian dispersal of the fauna has not been taken up for discussion until a year ago (1906) and then only with regard to the origin of the red deer in Norway.

II. The Red Deer

In calling attention to the case of the red deer which is confined to western Norway from Stavanger to Namsos (59°–65° north latitude) while entirely absent from the interior or eastern Norway, I indicated that it "doubtless forms a small-antlered race, or subspecies, of *Cervus elaphus*," but I did not name it, as our museum then did not possess a specimen of this form. My friend, Professor Einar Lönnberg has since confirmed its distinctness and called it *Cervus elaphus atlanticus* (*Ark. Zool.*, III, No. 9, 1906, p. 11).

In this article (On the Geographic races of red deer in Scandinavia) Lönnberg does not give a separate diagnosis of this form, but from the text the following distinctions may be gathered:

Swedish Deer (*C. elaphus* typ.).	Norwegian Deer (*C. atlanticus*).
Much larger.	"Much smaller size" (p. 3).
"Well-developed mane" (p. 3).	No well-developed mane.
Summer coat "dark reddish brown, almost chestnut, and the legs very dark sooty or blackish brown" (p. 3).	Summer coat "yellowish brown with tinge of grey and the legs much paler, slaty brownish grey" (p. 3).
Caudal disk "less pronounced . . . sometimes not much lighter than the flanks and although it is bordered by a darker shade towards the thighs this dark color never takes the shape of a black stripe" (p. 3).	Caudal disk "lighter, somewhat reddish yellow and bordered by blackish" (p. 3).
As a rule "larger skulls" (p. 3).	As a rule shorter skulls.
Nasals "transversely curved," "well visible, especially when the skull is seen from the side" (p. 5).	Nasals "much flatter so that they are when the skull is viewed from from the side, hardly, or not at all visible in front above the ends of the premaxillaries" (p. 5).
Nasals "as a rule decidedly longer," much less expanded and more convex posteriorly, the "combined greatest width of both nasals contained about 3 times (one specimen only 2⅞ times) in the length" (p. 5).	Nasals as a rule decidedly shorter, "much more expanded and less convex posteriorly" (p. 5); "width of both nasals . . . less than 2½ times in their length" (in hinds never more than 2¾ times) (p. 6).
Height of nose at the posterior end of the premaxillaries "exceeds 50 mm." (p. 7).	Height of nose "at the hind end of the premaxillaries does not attain 50 mm., but usually is less than 45" (p. 7).

"Antorbital vacuities much wider, as a rule 28 mm. or more"—the length (in hinds and young stags) 58–63 mm. (p. 7).	Antorbital vacuities much narrower, as a rule 19 mm. or less (21 mm. in one large specimen), the length (in hinds and young stags) 39–47 mm. (but in the very old specimen 55 mm.).
Orbital roof "more solid," "pierced by several foramina, none of which even attains half the size as that of the Norwegian deer" (p. 8).	Orbital roof "very thin and shows one comparatively very large foramen with a diameter of more than 10 mm.," sometimes considerably more (p. 7).

Several other differences are also noted, but the above are the principal ones.

Lönnberg's material consisted of five Swedish hinds and young stags and seven Norwegian hinds and young stags (p. 8) as well as one "very old and big stag" from Norway (p. 7).

In addition to this material he had the skulls of two adult stags (with five tines on each antler) from Invernesshire, in northern Scotland, which he thinks probably represent another independent subspecies "which suitably may be termed *scoticus*" (p. 11). With these he associates a female skull from Ireland in the Dublin Museum, though he intimates that there may possibly be important differences between the Irish and Scotch deer (p. 13). However, "as far as could be concluded from this single specimen the dimensions agree pretty well with those of the Scotch deer. Both are small-headed and short-nosed, with small antorbital vacuities and large foramina supraorbitalia as the Norwegian deer, but otherwise not so slender as that race." In these respects *Cervus scoticus* differs from the typical *C. claphus* of southern Sweden. From the Norwegian *C. atlanticus* it differs, as alleged, by the skull being less slender. This greater robustness, according to p. 10, is shown in the greater width of the skull just behind the premaxillaries, in the greater zygomatic width, and in the greater height of the maxillary, the Scotch deer in these respects agreeing with the Swedish deer, though in the last-mentioned character the Irish specimen is said to be partly approaching the Norwegian deer (top of p. 13). The main difference from the latter, and consequent agreement with the Swedish deer, is found in the Scotch and Irish deer having the nasals less flattened and less straight.

As described by him, the Scotch-Irish deer is intermediate between the Norwegian and the Swedish deer.

The U. S. National Museum has recently acquired in exchange with the Zoological Museum in Kristiania (through Professor

Robert Collett) a splendid stag of the west Norwegian deer which fully bears out the distinctness of this form from the typical Swedish *Cervus claphus*. At the same time, it shows that Lönnberg's material was not sufficient to establish the range of individual variation in the Norwegian deer, and, moreover, it most completely demonstrates the identity of the Scotch deer with that of Norway. The necessity for scrutinizing it more in detail is therefore obvious.

No. 143,179 U. S. N. M., an adult male, killed at Gloppen, Nordfjord, Norway (about 61° 45′ north lat.), on March 12, 1906, is consequently from the most typical and central part of the Norwegian habitat. It is a full-grown animal (pl. LXVII) with five points on one, and six on the other antler, though it is not very old as shown by the molars not being worn at all. The bez tine is a mere rudiment on one side, while on the other it is quite small, less than one third as long as the brow tine. The latter forms an obtuse angle of about 110° with the beam.

As might be expected, the skull is somewhat larger than those of the young Norwegian stags described by Lönnberg, the basicranial length being 341 mm. though not so large as his "very old and big stag" with the corresponding length of 352 mm.

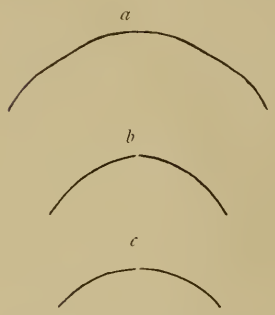

FIG. 124.—Diagram showing the curvature of the nasal bones of *Cervus atlanticus*, no. 143,179 U. S. N. M. Cross sections at three different points.

The nasals are comparatively short and wide, though not excessively so. The ratio between "the combined greatest width of both nasals" and "the length of the nasals," the one selected by Lönnberg to represent that fact, is 1 : 2.71. It consequently lies between the extremes of the two Scotch stags, as measured by him (p. 10), namely, 1 : 3 + and 1 : 2.6 respectively, as well as between his ratios for the seven Norwegian young stags and hinds, viz., 1 : 2.75 and 1 : 2.5.

But—the nasals are *not* flattened, as they should be if that character were a valid one for the distinction of the Norwegian deer. On the contrary, as will be seen from the accompanying diagram (fig. 124) which represents the upper surface of the nasals in cross section at their widest part (*a*), at a point opposite the posterior end of the premaxillaries (*c*), and at a point halfway between the two other points (*b*), the roof of the nose in this individual is very much convex. Moreover, as will be seen in the photograph of the profile of

SKULL OF CERVUS ATLANTICUS, ADULT MALE. No. 143179, U. S. N. M. VIEW FROM ABOVE

SKULL OF CERVUS ATLANTICUS, ADULT MALE. No. 143179, U. S. N. M. SIDE VIEW

the skull (pl. LXVIII) the nasals, when viewed from the side, are visible in front above the ends of the premaxillaries, fully as well, in fact, as in the Irish hind figured by Lönnberg (p. 12, fig. 6). Nor is the outline of the profile perfectly straight, as described and figured in Lönnberg's specimens. There is a decided curvature both in front and behind, so that this Norwegian stag appears to suggest the same "tendency to 'Rammsnase,'" as the two Scotch skulls described by Lönnberg (p. 10), a tendency apparently not shared by the Irish hind and as a character in these animals probably of no value whatever.

The antorbital vacuities are described by Lönnberg in the Norwegian, Scotch, and Irish speciments as essentially of the same size and shape. In our specimen they are rather large.

The supraorbital foramina are very large, one 15 mm., the other 18 mm., thus agreeing with the other Norwegian skulls as well as with the Scotch and Irish.

The other characters relied upon by Lönnberg are those of relative proportions and can best be discussed after I have given the requisite dimensions.

Our specimen (no. 143,179) measures as follows:

	Mm.
Basicranial length	341
Distance from anterior tip of premaxillary to orbit	211
Zygomatic width at the posterior end of jugale	146
Width of skull just behind premaxillaries	69
Length of nasals (average[1])	122
Greatest width of both nasals combined	45
Vertical height of nose at the posterior end of premaxillaries	58
Length of upper molar series (socket)	109
Width of antorbital vacuity	28
Length of antorbital vacuity	56
Longest diameter of foramen supraorbitale (average[2])	16.5
Height of maxillary above the foremost molar	40
Height of maxillary above the foremost premolar	69
Distance from lower orbital rim to last molar	46
Antlers, inside distance between beams at base of subroyals	508
Antlers, distance from burr to farthest point	578

Unfortunately, there are hardly any individual measurements of his Swedish and Norwegian specimens in Lönnberg's paper, most of the dimensions given being maxima and minima of the series, except in a few instances, so that it is impossible to include them in a comparative table, or to reduce them to the unit of one of the

[1] Right 120 mm.; left 123.5 mm.

[2] Right 18 mm.; left 15 mm.

dimensions. With regard to the Scotch and Irish specimens more specific data are given, though in the case of the two Scotch specimens I have been obliged to assume that he always gives the measurements in the same order, so that those mentioned first are to be regarded as belonging to the one individual, and those given last to the other. From his text I have thus culled all the individual dimensions, adding those of our specimen. Whenever the length of the facial part of the skull, as expressed by the distance from the distal end of the premaxillaries to the orbit (the dimensions selected by Lönnberg) is given, I have reduced the others to percentages of it. In the following table the actual measurement is given above the fraction line, the percentage below it.

COMPARATIVE MEASUREMENTS OF NORWEGIAN, SCOTCH AND IRISH DEER

	U. S. N. M. No. 143179. Norway. Adult Stag.	Hitteren, Norway. Very O'd Stag.	Hitteren, Norway. Young Stag.	Hitteren, Norway. Young Stag.	Scotland. Young Stag *a*.	Scotland. Young Stag *b*.	Ireland, Hind.	Southern Sweden. Young Stag.	Southern Sweden. Older Stag.
Basicranial length	341	352	303	310	311	319	301	330	373
	100	100			100	100	100		
Tip of premaxillaries to orbit	211	218			195	197	187		
	100	100			100	100	100		
Zygomatic width	146				139	143	135		
	69				71	72	72		
Width of skull behind premaxillaries	68				61	56	56		
	32				31	28	30		
Maxillary height above anterior molar	49				41	32	39		
	23				21	16	21		
Maxillary height above anterior premolar	65				60	60	55		
	31				31	30	29		
Orbit to posterior molar	46				42	45			
	22				22	23			

The substantial agreement of all the critical dimensions of the Norwegian, Scotch and Irish deer selected by Lönnberg is demonstrated by the above table. These deer are all equally short-faced, as already pointed out by him, but it is so far from the Norwegian deer always being the slenderer, that the specimen in our museum has decidedly the broader snout, while as to the maxillary height two of its dimensions fall inside the maxima and minima of the Scotch and Irish specimens, while one even exceeds their maxima.

Among the less important characters Lönnberg mentions (p. 8) the presence in the Norwegian deer seen by him a small foramen on the lower jaw below the anterior premolar, which is usually absent in the Swedish deer.[1] It is present only on one side in our

[1] Lilljeborg, *Sveriges och Norges Ryggradsdjur*, I, Däggdj., II, 1874, p. 794, mentions already the absence of this foramen in the Swedish deer.

specimen, and I may add that it is plainly visible in Lönnberg's figure of the Irish hind (p. 12, fig. 6).

It seems thus pretty clearly established that the name *Cervus elaphus scoticus* is only a synonym of *Cervus atlanticus,* and that my supposition of the Scotch and Norwegian deer being of the same extraction and different from the central European stock (*Amer. Natural.,* XXXV, 1901, p. 110) has been amply verified.

With this conclusion it would seem that Lönnberg's subsequent criticism (pp. 15–17) of my theory, that the deer immigrated into western Norway over an ancient Scoto-Norwegian land bridge falls to the ground. At the same time his own contention, that it came from south Sweden with the "*Ilex*-flora" and has died out in the intermediate territory, becomes untenable. I agree perfectly with his proposition (p. 18) that "the red deer went the same way as the flora did," but in the present essay I hope to show that the flora with which the red deer arrived in west Norway did not come *via* southern Sweden either. In his discussion of my theory Lönnberg complains (p. 15) that I did not specify explicitly the period during which the immigration into western Norway took place and surmises that I meant it to have occurred in preglacial time because of my view that some "members of the older Oriental invasion," as one of which I regard the ancestor of *Cervus atlanticus,* "joined the preglacial Siberian immigration in France," but my statement (*Amer. Natural.,* XXXV, 1901, p. 109) about this immigration taking "place early, probably before the first great glaciation reached its maximum" clearly refers to its entering eastern Europe during the early stage when "neither ice nor water had yet shut off the passage north of the Caspian Sea" and not to the time when its most westerly projected members reached Norway. I deliberately refrained from mentioning any specific time, because the Scandinavian geologists had not reached an agreement as to whether there has been one glacial epoch or several, or in the latter case whether the last glaciation in western Norway extended as far as the former, and in the paper referred to there was no opportunity to enter into any lengthy discussion of these questions. Under those circumstances I was very careful to avoid the word *interglacial* since in my opinion the invasion over a Scoto-Norwegian land bridge is a biologic occurrence which need not be affected either by the acceptance or the rejection of an interglacial theory.

After having stated "as an established geological fact that at the time of the first great glaciation the existence of any terrestrial

organic life in Scandinavia was utterly impossible "[1] and that "probably the situation was just as bad during the second glaciation," Lönnberg proceeds as follows: "In addition to this must be mentioned that from the time of the first glaciation and until the ice had almost completely melted away in the Ancylus epoch there was not only not a land connection between Scotland and Norway but the southern part of Scandinavia (including Denmark) was more depressed than it is now and thus the North Sea and Skagerak formed a barrier against the distribution of terrestrial mammals from Scotland to Norway even more effective than it is in the present day." Apart from a most decided reservation against the theory of the utter extinction of all higher terrestrial life in the entire Scandinavia during the two glaciations, and more especially during the second, being called "an established geological fact," since there is a growing opinion among glaciologists that there was a considerable area of ice-free land in western and northern Norway during the latter, I must insist that the question of a Scoto-Norwegian land bridge does not involve the rise of land in the southern part of the North Sea, Denmark, or southern Scandinavia. The land bridge in question connected much farther north, on the west coast of Norway certainly not south of 59° north latitude, while on the east coast of Scotland only the land north of 56°, including Shetland in the north and the Hebrides with northern and western Ireland in the west is included. It may be said in general that an interpretation of the biotic history of the glacial period in western Norway must always be defective if it is taken for granted that what happened there during that age was a mere synchronous repetition of what happened in the Baltic and in southern Sweden.

The other biotic and geologic considerations involved are treated of elsewhere in this paper and need not detain us here, but I wish to point out in this connection that my theory of the Scoto-Norwegian dispersal would not have been invalidated even if Lönnberg had been correct in considering the Scotch and the Norwegian deer subspecifically distinct. According to his view the former has more characters in common with the Central European deer, the

[1] Compare this with Kobelt's view in Die Mollusken der Palaearktischen Region, 1897, pp. 152–158.

The question whether the megaglacial period in Scandinavia was so excessively severe as indicated by Lönnberg I have barely touched upon in this essay, as it does not necessarily affect the main proposition I am defending. Probably everybody is agreed that it was severe enough to preclude the possibility of the majority of the biota here considered from having survived in Norway since preglacial times.

west Norway form being the more specialized type. Such a state of affairs would be quite consistent with my theory of the latter being the last link in an evolutionary distributional chain: Continental Europe—Scotland—Norway. Having been isolated from the Scotch ancestor for certainly more than ten thousand years, there would be nothing surprising if the Norwegian deer had evolved characters of its own, and it is even possible that the apparent tendency to flattened nasals in the latter is attributable to this long segregation.

III. The Celtic Horse

During the meeting of the Edinburgh Royal Society, on December 1, 1902, Professor J. Cossar Ewart read a paper "On a New Horse from the Western Islands, *Equus caballus celticus*" (*Nature,* LXVII, January 8, 1903, p. 239). It was described as a small pony, the principal character of which is that it agrees "with the asses and zebras in having no callosities on the hind legs." It was said to be "found in Iceland, Færœ, Barra, and other small islands of the Outer Hebrides, also in Connemara," northwestern Ireland. The inference from the brief communication is that the Celtic horse is an exclusively west European form as compared with the Arab and other eastern horses.

The color description, yellow dun with black fetlocks and stripes or fragments of stripes on back, legs, etc., at once called to my mind the west Norwegian pony, the so-called "Fjordhest" which is the predominant race of horse along the entire western coast of Norway, on the outer islands as well as in the fjord districts, while an entirely different horse, the "Dœlehest," or Gudbrandsdal horse occupies exclusively the interior and eastern part of the country. The almost identical distribution of this fjord horse with that of the west Norway red deer suggested a similar origin, and consequently I began to gather material for a further study of the question. As usual, I found the literary record very defective. The various races or species of recent horses were either treated from the osteological standpoint alone or from their outward characters alone, such as form, color, size, etc. It was also a surprise to find that a character as important as the horny callosity, the so-called "chestnut" on the hind legs which formerly has been held to be even of generic importance in separating the genus *Equus* from *Hippotigris* and *Asinus,* the zebras and asses, has been overlooked by almost all authors. Nor did I find in the literature any indication to what extent

this horny callosity is transferred to the hybrids between *Equus* and *Asinus*. On this latter point I was able to make observations on hundreds of mules to the effect that the callosity is nearly always transferred to the progeny. This is important, since it renders it almost certain that in hybrids among the more closely allied species within the restricted genus—or subgenus—*Equus*, the callosity will always be found, if possessed by one of the parents. In these days of universal crossbreeding of the domestic races for their "improvement" it has become very difficult to find a country horse of absolutely pure race except in the remotest part of mountain districts or regions otherwise difficult of access.

Fortunately, Tscherski in his excellent work on some fossil Asiatic horses[1] gave a clew by carefully describing both the external and the osteological characters of the "Tarpan," a small horse which until the middle of the last century was found wild in the steppes of south Russia. Not only did the tarpan lack the callosity on the hind legs, but in size and color also did it tally with the Celtic and the west Norway pony, and what is equally to the point, the skull "in its essential relative dimensions agrees with those of the Iceland horses."

The result of these preliminary investigations I summarized in a paper entitled "Den celtiske pony, tarpanen og fjordhesten," which was published in the June–July number of *Naturen* (Bergen), 1904, in which I urged the specific distinction of *Equus celticus* and suggested the extreme probability that all three horses mentioned, viz., the Celtic pony, the Russian tarpan, and the west Norway fjord horse belong to this species, and the various heavy European horses to another species which must stand as *Equus frisius* (Boddaert).[2] I also suggested that the fjord horse came to west Norway from Scotland as a descendant of the Celtic pony.

About the same time Professor Ewart published a more detailed

[1] *Mém. Acad. Sci. St. Pétersbourg* (7), XL, No. 1, 1892, pp. 257–383.

[2] Of which Fitzinger's *Equus robustus* and Nehring's *E. caballus* var. *germanica* are synonyms.

The Linnean *Equus caballus* is a collective name without indication of type specimen, of course. The restriction of the name, as practiced by the first revisor, must, therefore, be accepted, and this restriction it appears was undertaken by Fitzinger, in 1858, who reserved the name *E. caballus* for the group having the Arab for type. Now to restore the name to the horse occurring in eastern Sweden is clearly impracticable, as no well-defined form is restricted to that country and, moreover, would be contrary to all accepted nomenclatorial codes. The relationship of Fitzinger's *E. velox* to his *E. caballus* is one of the many unsettled questions in European hippology.

account of his new pony under the title "The multiple Origin of Horses and Ponies" (*Trans. Highl. Agric. Soc. Scotland* (5), XVI, 1904, pp. 230–268; abridged in *Nature*, LXIX, 1904, pp. 590–596). In this paper, which had not come to hand when I wrote mine, the characteristics of *E. celticus* are more elaborated, especially what he terms the caudal fringe, or "tail-lock," of the winter coat, a heavy covering of long hair at the root of the tail above. This he regards as the result of adaptation to a subarctic environment. Hence, it seems to me, its presence or absence in allied forms or varieties does not carry much weight as proving or disproving relationship. About the mane he says that it "is made up of a mesial portion (nearly twice the width of the entire mane in an Arab) consisting of strong dark hair, and of two lateral portions the hair of which are lighter and finer." He also mentions a flat-nosed variety in the Færœs, the Hebrides and in Shetland which, except in color, shape of the head, and occasionally the form of the hind-quarters, closely agrees with the typical Celtic pony. Some of these flat-nosed ponies are of a foxy-red color, others are dark brown.

A very important section of his paper is devoted to "The Norse Horse (*Equus caballus typicus*)." This he regards as having "centuries ago acquired the rank of a distinct species, or at least a well marked natural variety." "A typical specimen of the Norse variety is of a dark yellow-dun colour, with black 'points,' and a nearly black mane and tail" (p. 264; p. 595). "The space between the orbit and the nostril is relatively longer than in the Celtic pony" (p. 265; p. 596), it is consequently a longer-faced animal, in connection with which statement it is noteworthy that the forehead is said to be "not particularly wide." Several more differences are noted, but it is sufficient here to mention the last one given, viz., that the Norse horse differs "in having a complete set of ergots and chestnuts" (p. 265; p. 596); it has consequently the horny callosities of *Equus caballus*. Professor Ewart does not give the exact distribution of the Norse horse, but he mentions expressly that it occurs in the northwest of Scotland, and that "there is little doubt that it was introduced into Scotland from Scandinavia about the end of the eleventh or beginning of the twelfth century" (p. 264; p. 595). He finally concludes his comparison of the two types with the emphatic statement that "it is inconceivable that the Norse variety could . . . be regarded as an offshoot from the Celtic pony"!

Compared with my own conclusion, given above, that the Celtic pony and the west Norwegian horse belong to the same species, it would seem that Professor Ewart and I have come to absolutely diametrically opposite results. Yet, it only seems so, for I am willing to subscribe to every word of his conclusions with regard to the Norse horse he is speaking of. The explanation is, of course, that he does not refer to the west Norwegian horse I have been treating of, the true "fjordhest." His Norse horse is the "dœlehest," and these two I regard as specifically distinct.

There is nothing in Ewart's paper to indicate that there are two very distinct types of native horses in Norway, and yet no fact is better established. One of these was originally, and is even now to a great extent, confined to the west coast, the other to the interior valleys and the lowlands of the eastern part of the country (hence the distinctive names of fjord-horse and valley-horse). The latter being the heavier horse has in later years been introduced into the western districts in order to "improve" the coast race, and consequently numerous hybrids are now found in west Norway.

It was my good fortune to be able to examine a large number of typical fjord-horses during a visit to Bergen in 1905. I was very apprehensive lest the admixtures of foreign blood might have nearly obliterated the pure breed, but fortunately my fears were unfounded, there were enough unmixed, unimproved horses left.

To be brief and to the point, I found the fjord-horse to possess all the essential characters of *Eqvus celticus*, as given above, in which it differs from Ewart's "Norse horse." Its normal color is a pale buff, but also often mouse-gray; uniform dark brown specimens such as Ewart describes in his flat-nosed varieties of the Celtic pony, are also seen. The mane is bicolored, light on each side with a broad, black central part, exactly as described by Ewart in the typical Celtic; the tail is also only mixed with black. All these points are fairly well shown in the photograph (pl. LXIX, 1). The winter coat, especially in the animals of the outer coast which often, particularly in former times, have to pass the winter in the open air without much shelter, is rather long with long forelock and beard, and long hair at the base of the tail. The forehead is broad and the facial portion of the head short. The legs are rather slender and the hoofs small. And last, but not least, *the typical west Norwegian pony lacks the hind chestnuts,* the horny callosities on the hind legs, the main criterion of *E. celticus!* I examined a large number of farmers' horses in the city of Bergen on the regular

FIG. 1.—NORWEGIAN FJORD HORSE, EQVUS CELTICUS, IN BERGEN

FIG. 2.—NORWEGIAN FJORD HORSE, LOFOTEN VARIETY. MOUNTED SPECIMEN IN THE BERGEN MUSEUM

market days and was surprised to find how many were without a trace of these burrs. In the majority of the animals there were small, often very minute vestiges of callosities, and it was interesting to note how closely their smaller or greater size corresponded to the greater or lesser approach of the other characters to the type of the pure-bred horse. These were all common farm horses without pedigree, and the amount of admixture of foreign blood was a matter of conjecture. Only in one instance was I able to examine an *authentic* hybrid between alleged pure-bred parents. The specimen is now mounted in the Bergen Museum. It is a mixture of Nordfjord horse and Gudbrandsdal horse, and the longest diameter of the posterior callosities measures 23 mm.

In the museum at Bergen I found another highly interesting specimen which has a decided bearing on the question. I am, therefore, going to give some details derived from an examination, for the privilege of which I am greatly indebted to the curator of the division of vertebrates, Mr. James A. Grieg.

The specimen is one of the last survivors of a white variety of the fjord-horse formerly more common in Nordland and, more especially, on some of the Lofoten islands. A photograph of the mounted specimen (pl. LXIX, 2) shows what an extraordinarily long-haired creature it is, exceeding that of the Celtic pony figured by Ewart (p. 249, fig. 34; p. 593, fig. 5), the hair being distinctly curly, especially on the legs. Needless to say, *the hind chestnuts were absolutely lacking!*

The most interesting part of this specimen, however, is its skull. Unfortunately, we have no description of any skull from the type locality of *Equus celticus,* but Ewart's hints as to the relative width of the forehead and the length of the facial portion of the two horses indicate an agreement with the results which I have obtained.

The following measurements of the skull of the Lofoten horse are only those regarded by Tscherski as of particular importance.

Tscherski's number	Dimensions	Millimeters
1.	Basicranial length	456
3.	Distance from the middle of the occipital crest to the outer rim of the orbit at the point of greatest cranial width (Hintere Augenlinie, Nehring)	187
4.	Distance from the point between the median incisors to the outer rim of the orbit at the same point (Vordere Augenlinie, Nehring)	352
5.	Distance from the point between the median incisors to the nearest point of the anterior rim of the orbit	295

15. Distance from anterior margin of foramen magnum to the vomerine notch 118
16. Distance from vomerine notch to posterior margin of the bony palate 99
30. Greatest width between the outer margins of the orbits.... 216

Tscherski relies primarily upon the three cranial indexes elaborated by Nehring and himself for the expression of racial characteristics of the horses. They may be explained briefly as follows:

(1) The *Frontal Index* (Stirnindex, Tscherski; Index I, Nehring) expresses the proportional relation of the length of the skull to its width. It is obtained by dividing the basicranial length (dimension 1 of the above table) by the greatest width of the cranium at the orbits (dimension 30) and multiplying by 100. Skulls with a frontal index less than 227 are regarded as brachycephalic (breitstirnig, Tscherski), those with an index between 227 and 240 mesocephalic (mittelstirnig), and those above 24 dolichocephalic (schmalstirnig).

(2) The *Orbital Index* (Augenindex, Tscherski; Index III, Nehring) expresses the relation of the length of the facial part to the cerebral part of the skull by dividing dimension 4 by dimension 3 and multiplying by 100. The greater the resulting figure, the more long-faced is the horse and *vice versa*. This index is less reliable than the next which is intended to express the same relation, but it is utilized because only by it Nehring's numerous measurements become available for comparison, as his tables do not include dimension 5. Skulls with an index less than 190 may be regarded as short-snouted, with more than 190 as long-snouted.

(3) The *Facial Index* (Facialindex, Tscherski, p. 278) expresses the length of the snout by reducing the distance between orbit and tip of snout (dimension 5) to a percentage of the basicranial length. Tscherski does not state where he draws the line between short-snouted and long-snouted horses, but 65 or 65.5 probably expresses his idea (see p. 278).

These indexes in the Lofoten skull may be tabulated as follows:

Frontal index	217
Orbital index	188
Facial index	64.7

It will be seen, consequently, that this west Norwegian pony belongs to Tscherski's "small" horses (having a basicranial length of less than 460 mm.); that it is exceedingly brachycephalic; and that both according to the orbital and the facial indexes it is short-

snouted. This agrees substantially with the corresponding feature of the Celtic horse which, according to Ewart, has a broad forehead and a short snout.

It is interesting to note that the temperamental traits characteristic of the Celtic pony, viz., "keenness and speed, staying power and agility" (Ewart, p. 254) are the very ones attributed to the Norwegian fjord-horse.

It is at present impossible to decide whether the Celtic pony of western Norway came to that country in the wild state or domesticated.[1] But in either case, from what is now known of its geographic distribution, it must have come from Scotland. That it should have arrived from the southeast of Scandinavia with the "oak-flora," or with the dolichocephalic Teutonic race of man seems incredible, while the "dœlehest" unquestionably came with them that way. Ewart's ingenious explanation of certain characteristics of the Celtic horse and *his* (*i. e.*, eastern) Norse horse as indicating the latter to be a member of the forest fauna, the former, of the Steppe fauna (p. 263; p. 595), or as I should prefer to say, the heath or barren-ground fauna, is highly suggestive in this connection.

IV. Other Species of Mammals

It will be remembered that my theory of an invasion of western Norway from Scotland by those members of the older, or "first" Siberian invasion which had been able to penetrate so far westwards before the final disappearance of the Scoto-Norwegian land bridge, extended to the whole assemblage called "the Arctic fauna" by Sharff in his valuable book on "The History of the European Fauna." I also included the red deer, as already discussed above in detail, and the Norwegian lemming (*Lemmus*

[1] I have already (p. 461) alluded to the fact that I suspect a certain element of the population of west Norway, whose distribution is nearly identical with that of the red deer and the Celtic pony, of having arrived there from Scotland practically at the same time as the "Atlantic" biota and over the same land bridge. In Scotland the presence of a similar type during the stages following the megaglacial climax is also known. That this element of the Norwegian population may have arrived there during "interglacial" time is admitted by Hansen (Landnaam i Norge, 1904, pp. 299–300).

As for the domestication of the horse it is now regarded as conclusively proven by Piette that it was accomplished "during the late Pleistocene epoch" (*Nature*, November 29, 1906, p. 108). There would then seem to be a possibility that the people alluded to may have brought the pony with them in a domesticated state.

lemmus) which Scharff considered as belonging to the [second] Siberian invasion. It is characteristic of the past and present distribution of these so-called "Arctic" animals that besides Norway they inhabit Great Britain and Ireland, the Alps and the Pyrenees, or have been found fossil in these countries and south of these mountains. Species which at the present day *also* inhabit extensive areas in the Arctic regions to the east of Scandinavia may have entered this peninsula from the east and north over Finland, in which case the Scandinavian species would be of dual origin. Similarly, species *also* living to the south and southeast may have entered southern Sweden shortly after the recession of the ice cap and spread northward. Thus a triple origin even is conceivable, as members of the same species may have come by all three routes. Whether we may be able to verify this multiple descent in the animals now inhabiting the peninsula, depends in each individual case upon the degree of plasticity of the parental form and also upon to what extent the members of the various invasions have been able to interbreed *after meeting again* on Scandinavian soil. No critical examination of the fauna with this particular object in view and based upon sufficient material has ever been attempted. There are plenty of hints, however, in the literature of such multiple origin of several of the species involved. Thus Nilsson, in his Skandinavisk Fauna, Däggdjuren (2 ed., 1847, p. 444) refers to several Swedish forms of *Lepus timidus* and to the possible distinction of the north Russian *Lepus variabilis* as a separate form.[1] Barret-Hamilton recognizes two Scandinavian forms of squirrel (*Sciurus vulgaris; Proc. Zool. Soc. London*, 1899, p. 6). There are also indications that *Mus sylvaticus* in Scandinavia may be of multiple origin,[2] and similar hints are plentiful with regard to many of the other micromammalia.

The scientific record of these is very incomplete as yet, but in a

[1] Barrett-Hamilton, *Proc. Zool. Soc. London*, 1900, pp. 88–91, refers to two of Nilsson's hares as *Lepus timidus* and *Lepus timidus collinus*, apparently considering the latter equivalent to the supposed larger northern form represented by the two large north Russian skulls examined by him. In this I think he is mistaken, for Nilsson expressly says that his *Lepus borealis*, with which he synonymizes his earlier *L. borcalis collinus* is a smaller form than his *L. borcalis campestris* (= *L. canescens*). The latter is from southern Sweden however. The large north Russian form, possibly extending into northern Sweden, should probably stand as *Lepus timidus variabilis*. See also Lilljeborg, *Sveriges och Norges Ryggradsdjur*, 1, Däggdj., 1874, pp. 420–422.

[2] Barrett-Hamilton, *Proc. Zool. Soc. London*, 1900, p. 405.

few cases enough is already known to indicate the probable meaning of the facts thus far recorded. Among these the case of the red-backed mice of the subgenus *Evotomys* is the most illuminating. In 1900 Gerrit S. Miller, Jr., published a preliminary revision of the group (*Proc. Washington Acad. Sci.*, II, pp. 83–109) based on 301 specimens from the regions with which we are here concerned. In northern and western Europe he distinguishes 10 forms belonging to three separate sections, viz.:

(*a*) *E. rutilus* which inhabits Arctic Asia and Europe west to Tromsœ, in Norway.

(*b*) A second section consisting of three allied but geographically disconnected species:

(1) *E. norvegicus,* from Norway north to Saltdalen (specimens examined, however, with one exception, all from Bergen Stift);

(2) *E. nageri,* from the Alps; and

(3) *E. vasconiæ,* from the Pyrenees.

(*c*) The third section embracing the species *E. hercynicus* (=*E. glareolus* Auctorum), with five geographically connected subspecies, as follows:

(1) *E. hercynicus hercynicus,* from Germany;

(2) *E. hercynicus helveticus,* from the lowlands of Switzerland;

(3) *E. hercynicus rubidus,* from the coast countries bordering the North Sea on the south;

(4) *E. hercynicus brittanicus,* from England and Scotland; and

(5) *E. hercynicus suecicus,* from eastern Sweden.

The distribution of the *nageri*-group (*b*) strongly suggests that of *Lemmus lemmus,* the variable hare, the reindeer, the ptarmigan, and several of the other animals of the same fauna, while the *hercynicus*-group (*c*), in turn, coincides with a large assemblage of species which entered Sweden from the south and also extended into non-boreal Britain. The only serious deficiency in the range of the *nageri*-group, as known to Miller in 1900, was its absence in Great Britain. That this discrepancy was only due to the imperfect status of the European faunal record was shown three years later by Barrett-Hamilton (*Proc. Irish Acad.*, XXIV, Sec. B, pt. 4, September, 1903, pp. 315–319) who described the new species *Evotomys skomerensis,* from a small island off the southwest corner of Wales, as "closely related to *Evotomys norvegicus* Miller, of Norway, *E. nageri* (Schinz) of the Alps, and *E. vasconiæ* Miller, of the Pyrenees," and "almost indistinguishable from those of

Boreal Europe." He suggests finally that "we may yet find amongst the Welsh Mountains further colonies of these Boreal Voles," and I might add that I would not be surprised if they also were to be found in the northern highland of Scotland.

The invasion of the ancestor of *Evotomys norvegicus* into Norway from the west is thus a distinct zoogeographical probability.

Were the various forms of the common field vole (*Microtus agrestis*) to be worked up with as ample material and painstaking skill as the red-backed mice, it is probable that parallel and equally suggestive results would be obtained, since there are enough indications pointing in that direction. But much collecting must be done in many places before anything reliable can be accomplished.

There are some points in the distribution of two of the mammals already mentioned to which I would call special attention, viz., the lemming (*Lemmus lemmus*) and the reindeer (*Rangifer tarandus*). They are now chiefly inhabitants of the mountain plateau of the Scandinavian peninsula, the former extending from southwestern Norway to Russian Lappland but not reaching east beyond the White Sea, the latter at the present time chiefly confined to the Norwegian fjells south of Trondhjemsfjord, while a small herd of wild reindeer is still found in West Finmark. Both animals show a decided western distribution in the southern part of the peninsula.

The range of *Lemmus lemmus* is such that there is no probability of a multiple origin. The fact that it is not found east of the White Sea precludes its having come into Scandinavia from the northeast. Its fossil history, on the other hand, speaks against it having entered from the south.[1] Furthermore, it has been found fossil at the base of the Alps and in British pleistocene deposits, and remains of lemmings of the Norwegian type have recently been found by Dr. Gadow in a cave in Portugal. The latter find shows pretty conclusively that this species belongs to the "first Siberian" invasion.

The wild reindeer (*Rangifer tarandus*), on the other hand, has almost certainly come into Scandinavia by several different routes. One form entered from the south and is now found fossil only in

[1] Winge has recently shown (*Vidensk. Meddel. Naturh. For. Kjöbenhavn*, 1904, p. 223) that the record of lemming from late glacial deposits in Denmark is erroneous. It is interesting to note that the ermine, or stoat (*Putorius ermineus*), another of the "Arctic" animals, is likewise absent in these deposits. Professor N. O. Holst, in a recent letter (January 22, 1907), informs me that these species have not been found fossil in Scania either. I may add that the polar fox (*Canis lagopus*) also appears to be absent.

southern Sweden. Another probably came from the northeast over Finland and northwestern Russia, the last remnants being found in a small herd in West Finmark. Finally, the distribution of the fossil remains of the barren-ground form in Ireland and Britain and the occurrence of this form in Norway make it probable that this species *also* reached the latter country from the west. It will be noted that I use very vague expressions. The fact is that no critical studies of the various "herds" in this region and of the fossil remains from the adjacent countries have ever been made[1] It is always taken for granted that the Scandinavian reindeer is a homogeneous, monophyletic species, and even the skeletons and skulls of tame Lapp reindeer have been used for comparison without reservation, notwithstanding the possibility that the latter *may* represent a fourth, probably Siberian race comparatively recently introduced by the Lapps. The whole question, moreover, has been made extremely intricate by the mixing and hybridizing of the "herds." Thus the northern, or Finmark, herd has been in contact with the Lapp tame reindeer for centuries and is probably greatly mixed in consequence. Of late years immense flocks of the same kind of tame reindeer have been introduced on the western plateau of southern Norway with the result that pure-bred wild reindeer are getting to be scarce.

Finally a word about the mammoth (*Elephas primigenius*) which plays such a conspicuous rôle in pleistocene history. A single small molar of this animal has been found among the gravel in the bed of a stream at Skjervasæter, in Vaage (Brögger, Norge i 19 Aarhundr., 1, 1900, p. 23, fig. 24), the only find of this kind in Norway. Brögger regards this as evidence of an ice-free interglacial

[1] Hansen (Landn. Norge, 1904, p. 291) speaks of the reindeer found fossil in south Sweden as resembling the "American variety" [woodland caribou?] and not their "relatives farther north" in Scandinavia. Professor Holst, however, writes me as follows: "The antlers of the reindeer are regarded here [in Stockholm] as useless in the diagnosing of any definite varieties. Such horns are not seldom found in Scania *under* the peat in the late-glacial clay or 'gyttja.' The museum of the Swedish Geological Survey possesses a multitude of such horns (cast off) and I myself have collected a considerable number. I have been able to demonstrate that cylindric and palmate forms occur together, and Professor A. J. E. Lönnberg has told me that in the collections from east Greenland he has found plainly cylindric and decidedly palmate forms mixed among the horns of the now-existing east Greenland reindeer. It is therefore scarcely likely that definite results with regard to the various varieties of reindeer will be reached until skulls shall be forthcoming."

period in Norway. The district of Vaage is not situated on the west coast, yet I have but little doubt that the ancestors of the mammoth which came to grief there immigrated to western Norway from Scotland over the Scoto-Norwegian land bridge. I will emphasize here that *Elephas primigenius* has been found fossil not only in Scotland, *but also in Ireland,* thus adhering to the general distribution of most of the "Atlantic" species we are dealing with. It "is most abundantly found in all the British Pleistocene deposits from the Forest bed of Norfolk upwards. . . . It is one of the few Pleistocene species that have been found in Ireland. The animal must have lived in Britain in vast numbers, and for a long time."[1]

The Vaage district is directly on the line between Dovre, Lom, and Nordfjord. Nordfjord, on the west coast, is nearly in the center of the area which in Norway must have constituted the northeastern abutment of the Scoto-Norwegian land bridge. It is probably along the same route that the "Arctatlantic" plants penetrated into the adjacent interior plateau regions of Norway where they form such a conspicuous part of the flora.[2]

The occurrence of the mammoth in connection with this particular element of the flora is highly suggestive.

V. Two "Atlantic" Species of Birds

That various species of land birds occasionally visit west Norway from Scotland there is ample evidence, I need only mention *Motacilla boarula* and *M. raii.* That others migrate regularly back and forth between the two countries is also fairly well established. The former, as a rule, do not seem to establish colonies,[3] and with regard to the latter we have only the theory to go by that they migrate along their ancient line of dispersal. Such a theory, if unsupported by evidence of a former land connection, would be worthless, but

[1] W. Boyd Dawkins, Brit. Pleistoc. Mamm., 1866, Introd., p. xxxiii.

[2] See Wille, Invandr. Arct. Flora Elem. Norge, in *Nyt. Mag. Naturv.,* XLIII, 1905, p. 337.

[3] Mention should be made of the fact that the black-backed English wagtail (*Motacilla alba lugubris*) breeds, at least occasionally, in western Norway near Stavanger and Bergen according to Collett (*Nyt Mag. Naturv.,* XXXV, 1893, p. 104), a reference which seems to have been overlooked by Hartert in his Vögel der Paläarktischen Fauna. No weight is attached to this invasion which seems to be quite recent, a surmise which is strengthened by the facts that the bird is only an occasional visitor to the Shetlands, that the typical *M. alba* is the breeding bird of Ireland, and that it also breeds here and there in England and Scotland.

in this case the two theories mutually support each other and thus, to some extent, possess the merit of corroborative evidence.

There are two birds, however, the geographical distribution of which is so interesting and bears so directly upon the attempt made in this essay to demonstrate the existence of a well-assorted and peculiar biota having made its way from Scotland to west Norway since the climax of the glacial epoch, that their case deserves a closer scrutiny in this connection, especially as their geographical distribution has never been viewed from this standpoint before. It is somewhat parallel to that of the ptarmigan (*Lagopus mutus*), but as I have already referred to that species before in a similar connection (*Amer. Natural.*, XXXV, 1901, p. 106) and am going to allude to it again in a subsequent chapter of this paper (p. 488) I shall not mention it further here.

The first of the two birds is the twite, or "mountain linnet" (*Cannabina flavirostris*). As a breeding bird it is absolutely confined to Ireland, northern Great Britain and western Norway. Professor Newton (Yarrell's Hist. Brit. Birds, 4 ed., II, 1876, p. 161) in speaking of the distribution of this bird in England says that "it breeds in some abundance in the more hilly districts of the Midland Counties—Hereford, Salop, Stafford, Derby and Chester, as well as in North Wales and the Isle of Man, and on elevated moorlands in the higher glens with increasing frequency northward from Lancashire and the West Riding of Yorkshire to Shetland, though in some districts it is rather scarce, and its stronghold in the west of Scotland is the Outer Hebrides. In Ireland it is found from north to south, and probably breeds in suitable localities throughout the island." In Norway it breeds rather commonly along the west coast from Jæderen northward to Lyngen (70° north latitude). Collett "found it most numerous on the islands of Bergen Stift, and on the Trondhjemsfjord and on Hitteren." Small colonies have also been found in the Alpine belt of the western mountains (Collett, *Nyt Mag. Naturv.*, XXXV, 1893, p. 83).

The twite is not a regular migratory bird, but belongs to the category of winter birds which Seebohm aptly calls "gipsy migrants." It does not winter only in England, but in Norway as well, occasionally even as far north as Trondhjem, though many extend their irregular wanderings to the continent.

Cannabina flavirostris although now more or less confined to the islands and coasts of the north Atlantic is not originally a maritime bird, and it is very extraordinary indeed that we do not find it, or a representative of it, in the mountain districts of central and

southern Europe. It is hardly necessary to remark that we have no fossil evidence of its former occurrence there, yet it can scarcely be doubted that at one time its line of dispersal from the east lay in that direction and that, like the lemming and many other species of the same invasion, it became extinct in the Alpine regions of the south. The evidence of such a connection with Asia is furnished by the slightly different form, *Cannabina brevirostris,* which is so closely allied to it that Hartert has connected the two forms trinominally in spite of the hiatus of 2,000 statute miles (3,220 km.) between their breeding areas. This Asiatic form of the twite extends from Caucasus through Persia, Turkestan and Tibet into Manchuria, and it is inconceivable that the two forms have not been separated in comparatively recent times.[1]

The second species is the rock pipit, *Anthus petrosus,*[2] which doubtless is only a subspecies of a circumpolar species and for that reason will be known by many ornithologists as *Anthus spinoletta petrosus.* The group of forms embraced by them in the term *A. spinoletta* is represented in subarctic North America (I speak only of the breeding ranges) by *A. pensilvanicus,* in eastern Asia by *A. japonicus,* in central Asia, west to the Caucasus by *A. blakistoni,* while a special form *A. coutellii* is peculiar to the mountain regions of Persia. "*A. spinoletta spinoletta*" to them is the name of the bird which "during the breeding season inhabits the mountains of central and south Europe, the Vosges, the entire region of the Alps up to an altitude of 2,500 m., the Schwarzwald, the Hartz Mountains, the Sudeten, the Thuringian Forest, the Pyrenees, the high mountain systems of Spain, the Karpathians, and the mountains of the Balcan Peninsula and Asia Minor, as well as the high mountains of Italy and surely also Sardinia" (Hartert, Vög. Paläarkt. Fauna, III, 1905, p. 280). In all these localities the water pipit, or Alpine pipit, as Seebohm has proposed to call this type, is confined to the moun-

[1] Another closely allied form from Kashmere has been described recently by Hartert. It will stand as *Cannabina flavirostris stoliczkæ,* or *C. brevirostris stoliczkæ* according to the view as to the degree of distinctness of *C. brevirostris.*

[2] This is the bird usually known to European ornithologists as *Anthus obscurus.* The name *Alauda obscura* given to it by Latham, in 1790, is antedated by the two years older *Alauda obscura* of Gmelin (Syst. Nat., I, ii, 1788, p. 801) which is an entirely different bird. Montagu's *Alauda petrosa* (*Trans. Linn. Soc. London,* IV, 1798, p. 41), based on the same specimen which served Latham as type of his *A. obscura,* must, therefore, be adopted as the oldest available name.

tains. As we approach the north and west we meet forms which breed at the level of the sea. Thus a race rather lightly spotted with black and suffused with rust color on the breast in the breeding plumage, *Anthus littoralis,* extends from Denmark along the west coast of southern Sweden to Hvaler, a group of islands at the southeastern corner of Norway. On the other hand, a heavy-spotted form, without a distinct wash of rufous on the breast, *A. petrosus,* makes its appearance as a breeding bird on the coasts of northern France, extending northwards through Great Britain and Ireland to the Scottish islands and to western Norway north to Finmarken. An extreme race of this form occurring in the Færœs has recently been distinguished as *A. spinoletta kleinschmidti* (Hartert, Vög. Paläarkt. Fauna, III, 1905, p. 284).

The rock pipit, as stated, breeds along the coasts of the British islands. Saunders (Illustr. Man. Brit. Birds, 1889, p. 135) says that "in Scotland it is abundant in suitable localities, especially in the west, and it is equally common in Ireland." Dresser quotes Robert Gray to the effect that it is common "on all the northern islands, including the outer Hebrides, Monach Isles, Haskar Rocks and St. Kilda," and continues: "Mr. Dunn found it very abundant in all parts of Shetland, and Captain Clark-Kennedy informs me that he has met with it very abundantly along the shores of Caithness, Sutherland and others of the northern counties of Scotland, and especially numerous in the Orkneys" (Birds of Europe, III, p. 344).

In Norway it breeds commonly on all the islands and along the entire outer coast up to Varangerfjord in East Finmark, but it never breeds in the interior of the country.

With the Baltic rock pipit (*Anthus littoralis*) breeding in the extreme southeastern corner of the country we have in Norway, consequently, two forms of rock pipit,[1] although some authors seem to think that the typical *A. petrosus* does not occur there and that the

[1] To Professor Robert Collett belongs the honor of having discovered and repeatedly called attention to this fact (*Nyt Mag. Naturv.,* XXIII, 1877, p. 144; XXVI, 1881, pp. 306–307), naming the west coast form typical *A. obscurus* [= *petrosus*] and the "variety occurring in the southern part of Sweden," with "light rusty yellow and more unspotted lower surface," *A. rupestris.* Nilsson, however, gave the latter name only as a substitute for *A. obscurus* considering, as he did, the latter ineligible because there are several species of *Anthus* to which the name *obscurus* applies. Brehm's *Anthus littoralis* (*Lehrb. Naturg. Europ. Vög.,* I, 1823, p. 239) is based upon specimens collected on the island of Oehe, on the east coast of Schleswig, and is apparently the south Swedish and Danish bird.

bird inhabiting "the coasts of Scandinavia" is the *A. spinoletta littoralis* (Hartert, Vög. Paläarkt. Fauna, III, 1905, p. 284).

The distribution of these forms in Norway plainly indicates the way by which they entered the country, *A. petrosus* from the west, *A. littoralis* from the south.

The rock pipit in western Norway is a "gipsy migrant" like the twite, many individuals wintering along the coast at least as far north as the Trondhjemsfjord (Collett, *Nyt Mag. Naturv.*, XXVI, 1881, p. 307), while others undertake more or less extended wanderings in various directions.

VI. The "Atlantic" and "Arctatlantic" Plants in Western Norway

The late Professor Axel Blytt, in his celebrated paper on the immigration of the Flora of Norway (*Nyt Mag. Naturv.*, XXI, 1876, pp. 279–362) clearly distinguished two elements among others, in the flora peculiar to western Norway, viz., those plants which extend from Stavanger northwards and which are chiefly characteristic of the coast between the latter city and Kristianssund, and those which do not occur north of Stavanger. The former he named (p. 339) the *Atlantic,* or Bergen coast plants, the latter the *Subatlantic,* or Kristianssand coast plants. These he believed to have come to western Norway "over the sea from the southwest," though the context shows that he meant from Denmark. Among these *Ilex aquifolium,* the holly, is one of the most conspicuous plants and occurring, as it does, from Arendal to Kristianssund, consequently covering the range of both the Atlantic and the Subatlantic plants, the combined assemblage is often called the *Ilex*-flora. This nomenclature is very unfortunate since, as I hope to show, the two categories probably have arrived in Norway from two different directions, the former from Scotland, and the latter from Denmark.

As already stated, the Atlantic plants in western Norway have their main distribution between Stavanger and Kristianssund, or roughly between 59° and 63° north latitude, and are mainly confined to the coast without even penetrating into the deeper western fjords, but many species have extended their range considerably further north and south so that a few of them have even reached the western coast of Sweden. About 60 species of vascular plants are regarded as belonging to this category.

The Subatlantic flora is probably equally rich in species and oc-

cupies the southern coast from Stavanger east to the Swedish frontier, the center of distribution being between Mandal and Arendal.

The essential difference between these two groups of plants is not one of lesser or greater hardiness and consequent latitudinal difference in south-and-north extension. It is rather one of general distribution, the Subatlantic species being of more eastern affinities and range than the Atlantic ones, indicating a previous history of evolution and dispersal entirely different in the two groups. This is not only shown in their having two distinct centers of distribution in Norway, but also by their respective ranges in Denmark and especially in Ireland. All the true Atlantic species in western Norway are also found in northern Scotland and almost all in northern and northwestern Ireland. The Subatlantic species, on the other hand, as a rule, do not reach Scotland and some even miss southern Ireland.

Blytt's conclusions were based chiefly on the distribution of the vascular plants. Since his time the bryophytes of Norway have been studied more in detail, and the results yielded by them for our purpose are even more conclusive, especially the recent studies of the Norwegian hepaticæ (liverworts) by Kaalaas (*Nyt Mag. Naturv.*, XXXII, 1892–1893, pp. 1–490) and by Jörgensen (*Bergens Mus. Aarb.*, 1901, No. 9 and No. 11). According to them there are no less than 27 species of "Atlantic" hepaticæ on the west coast of Norway, as follows:

Lejeunea calcarea.
Lejeunea ulicina.
Lejeunea ovata.
Lejeunea patens.
Radula aquilegia.
Radula carringtonii.
Porella radicata.
Porella platyphylloidea.
Pleurozia cochleariformis.
Pleurozia purpurea.
Lepidozia pearsoni.
Lepidozia pinnata.
Adelanthus decipiens.
Kantia arguta.
Saccogyna viticulosa.
Herberta adunca.
Scapania gracilis.
Scapania planifolia.
Scapania ornithopodioides.
Plagiochila punctata.
Jungermannia orcadensis.
Jungermannia atlantica.[1]
Jungermannia ovata.
Jungermannia doniana.
Nardia compressa.
Gymnomitrium crenulatum.
Fossombronia angulosa.

[1] This has not been recorded from Britain, as yet, but since it has been credited to the Færöes by Jensen (Bot. Færöes, I, 1901, p. 133) it will probably eventually be found in Scotland also, if really an Atlantic species.

All of these, except *J. atlantica,* have been found in Great Britain and Ireland and no less than seven, or 25 per cent., are thus far known only from western Norway, Scotland and Ireland (two also from the Færöes and one as yet only from the latter and Norway). Several of the others extend only to western France.

Blytt also distinguished in the Norwegian flora another element which he termed specifically the "Arctic" plants, generally supposed to have entered the Scandinavian peninsula gradually from the south, immediately following up the melting of the great ice cap. In a recent paper, however, Professor N. Wille[1] has shown most conclusively that this theory is not borne out by the facts and that the "Arctic" flora, so far from being of homogeneous origin, consists of at least two very distinct elements, one which is of decided Siberian relationship and which entered northern Norway from the east *via* the Kola peninsula, and another which he believes to have come from Greenland *via* an Iceland-British-Norwegian land bridge and to have survived the last glaciation on an ice-free coast along western and northern Norway. He consequently reaches a conclusion agreeing in many points with that of Dr. Hansen (see *antea,* p. 461). He sums up his results as follows (p. 337): "The facts at hand, therefore, seem to me to indicate that during the last ice-period there lived in Norway a high-arctic vegetation on an ice-free coast which must have extended as far south as the Sognefjord [61°]. Later on several species of high-arctic plants, which in the course of time immigrated into northern Scandinavia from Russia and Siberia, have pushed southward to a lesser or greater extent. As the land ice retreated from the south and east after the conclusion of the last glacial epoch a subarctic rather than an arctic vegetation followed from Sweden into southeastern Norway."

The element of the west Norwegian flora, which it may be convenient to designate as the "Arctatlantic" element, must consequently have come from the west, from Scotland, and it is highly significant to note that Wille, whose studies of the fresh-water algæ of the Færöes have been quoted in defense of their reaching these islands across the sea[2] now admits the probability of a land bridge (p. 318) and the insufficiency of explaining the presence of the Arctatlantic element *as a whole* upon the theory of accidental dis-

[1] Om Indvandringen af det Arktiske Floraelement til Norge, in *Nyt Mag. Naturv.,* XLIII, 1905, pp. 315–338.

[2] See *postea,* p. 490.

persal (p. 319). It is also to be noted that he specifically excludes Jæderen (p. 337) and the coast south of it from the *direct* line of invasion and shows that the Arctatlantic plants reached that part of southwestern Norway at a much later period.

VII. The Way of Dispersal into Western Norway

It is clear that if a more or less ice-free land bridge existed between northern Scotland and west Norway during the glacial period, a whole complex biota must have crossed it. Animals and plants are so closely bound together that the movement of the fauna must necessarily depend upon that of the corresponding flora. Whether such an invading biota is to be composed of many or few species is determined by several circumstances. Of these the length of time during which the land connection lasted, the diversity of environment, including climatic conditions, and the distance in space from the center whence the biota emigrated, are the principal factors. A consideration of the simple fact that some species spread much slower than others shows this contention to be true. Therefore, if we remember that part of the association of plants and animals, which in this paper it is suggested immigrated into western Norway by a Scoto-Norwegian land bridge, at one time must have had its center of distribution in western continental Europe before entering England, while a large portion of the animals are supposed to hail even from western Asia, it will be seen that a considerable distance had to be traversed and that western Norway lies at the extreme end of a long and tortuous route. Small wonder if the fauna and flora are found to be somewhat attenuated when reaching their farthest point. Many species in this westward and subsequent northward and finally eastward push must have lagged behind, and in corroboration of this theory we should expect to find conspicuous forms which were unable to keep up with the procession and thus failed to reach western Norway before the final submergence of the land connection. As a matter of fact, there are many such species, but it is not necessary to refer here to others than the muskox (*Ovibos moschatus*) and the banded lemming (*Dicrostonyx torquatus*) which are not found in Norway, living or fossil.

On the other hand, it must be emphasized that the species and forms referred to above are not the only ones which came that way, but they are only those of which we know that they differ structurally from the other individuals which may have invaded the peninsula from other directions. Many plants and animals of gen-

eral distribution and of uniform morphological characters throughout their range probably accompanied the more easily differentiated members of the various invasions and meeting again in Scandinavia resumed their former continuity. Thus the pine (*Pinus sylvestris*) may have come to Scandinavia by two different routes, from the south and from Scotland.[1] As far as I know, a thorough comparative study of the morphological characters of the Scotch and west Norway pines has not been made to ascertain if any (possibly quite minute) differences exist which distinguish them from the east Scandinavian pine, although from experiments made in western Norway with seeds from the Scotch tree there seems to be at least some physiological similarities between them as distinguished from the eastern pines.

Slight morphological differences between Scotch and Norwegian forms, however, need not mean that they have no genetic relation. It depends upon other circumstances how such differences may be interpreted. While undoubtedly many species may have retained their identity in spite of the segregation on both sides of the North Sea since glacial times, others more plastic, as the phrase is, may have been differentiated into diagnosable races on account of a similar geographical separation during the same space of time. Take as an example the case of the tundra ptarmigans (*Lagopus mutus* and *L. rupestris*) which ornithologists consider different species. The former extends in Scandinavia east to the White Sea, the latter from there on eastwards, while in the west and south *Lagopus mutus* still lives in Scotland, the Alps and the Pyrenees. At least two of these isolated colonies of the ptarmigan have become slightly differentiated, viz., the Scandinavian and the form inhabiting the Alps. Whether the Scotch and Pyrenean ptarmigans also show the effect of the long segregation is not known but matters very little in the present connection, since the general distribution of the collective species is fair proof of its belonging to the whole assemblage of animals and plants which came to Norway from the west.

However, granting that such a biota invaded Norway from the direction of Scotland, does it necessarily follow that it traveled over a continuous land bridge?

In attempting to answer this question it is imperative to discuss the various categories composing the flora and fauna involved.

[1] Analogous to the dual origin of the spruce (*Picea*) in eastern and northern Norway.

Beginning with the plants, we have two extreme parties among the phytogeographers, those who insist upon the slow and gradual dispersal of the flora over land connections, and those who, like Warming and Sernander, see no difficulty in assuming that entire plant associations by the aid of wind, ocean currents, migrating birds, etc., are enabled to cross extensive bodies of salt water, such as the Skagerak, the North Sea, or even greater stretches of open ocean. These diametrically opposed views have led to a very instructive discussion about the dispersal of the flora of the Færöes, which it will be profitable to review here in some detail, because of the direct bearing it has upon our own studies.

In the "Botany of the Færöes based upon Danish Investigations," pt. I, pp. 112–119 (Copenhagen and London, 1901), C. H. Ostenfeld has a chapter on "The Immigration of the Flora," in which he states as his belief derived from a study of the phanerogams and pteridophytes and a full discussion of the various theories, that apart from a few species "introduced by the agency of the winds (and birds?)," "the chief part of the present flora of the Færöes has migrated across a postglacial belt of land" (p. 118) from Scotland, with the flora of which it "bears a wonderful resemblance." He thinks that "if it had been a question of immigration across the sea, the flora taken as a whole would hardly have been so very much like that of Scotland. It would have consisted of fewer species" (p. 115). The above conclusions were based upon the vascular plants, with the exception of the difficult group of the *Hieracia* which were studied by H. Dahlstedt. From the latter's account (Bot. Færöes, pt. II, 1903, pp. 625–659) I quote the following:

"Usually the different forms have not a wide geographical distribution. I am therefore of opinion that the study of the *Hieracia* of a single district in its relation to the neighbouring floral districts ought to be particularly useful as a contribution towards the solving of various plant-geographical questions. This has become still more clear to me by studying the *Hieracium*-flora of Scandinavia. I think that it will more particularly be of great help to us in determining the ways by which a flora of a land immigrates, and also the relative time for its immigration. The composition of the *Hieracium*-flora of the Færöes confirms the opinion expressed by C. H. Ostenfeld regarding the origin of the rest of the phanerogamous flora" (p. 626).

"It is an interesting fact that the Atlantic element in this genus

is so strongly represented in the Færöes. The presence of this element lends considerable weight to the theory of a postglacial land connection, which perhaps existed much longer than we have hitherto believed, judging from the other data" (p. 628).

Several years before the above conclusions of Ostenfeld and Dahlstedt were published Professor N. Wille, in a paper on the fresh-water algæ of the Færöes and on the modes of dispersal of these algæ in general (Botaniska Notiser, 1897) argued for their dispersal over the open sea chiefly by the aid of wind and, especially, migratory birds. F. Börgesen who worked up the fresh-water algæ for the Botany of the Færöes (pt. 1, 1901, p. 202) quite agrees "with Wille in thinking that the flights of birds which yearly take up their abode in the Færöes, or pass the islands on their way northwards *could*[1] very easily have conveyed to the islands the fresh-water algæ-flora—and *perhaps*[1] the whole of the flora—which is found there" (p. 202). In this conclusion he is fully sustained by Professor Eug. Warming who in the final chapter, "the History of the Flora of the Færöes" (Bot. Færöes, II, 1903, pp. 660–681) says: "I regard a postglacial land connection *very improbable,* and *not necessary* for the immigration of the Flora, which may be assumed to have immigrated across the sea" (p. 664). He admits, however, that "it is somewhat difficult to find evidence *against* the existence of a land connection, but it appears that one may be obtained from the *fauna of the Færöes.* It contained originally no wild terrestrial mammals, neither foxes, hares, moles, nor mice" (p. 670). He also finds unquestionable evidence in the flora, viz., the presence of the many temperate European or Atlantic species on account of the severe climatic conditions necessarily resulting from a land connection, although he apparently considers this objection valid only "were the bridge to be continued uninterruptedly to Greenland" (p. 671).

The belief in a postglacial land connection between the Færöes and Scotland has been particularly strong in the latter country and apparently, Warming's arguments have not had any great effect there (see the review of his article in the *Scottish Geographical Magazine,* XX, February, 1904, p. 98).

The net result of this discussion to us is a confirmation of our previous conviction that plants, as a rule, do not furnish an infallible

[1] Italicized here.

[2] It is well to recall that Professor Wille has since apparently changed his opinion about the land bridge (see *antea,* p. 486).

proof of an uninterrupted land bridge. It has been shown that some plants travel considerable distances across the ocean and become established, "remember Jan Mayen"! to use Warming's expressive and effective slogan. Jan Mayen island is located 240 miles (450 kilometers) from Greenland, the nearest land, exactly the distance between Scotland and western Norway, and it is about as certain as such an assertion can be, that its 39 vascular plants have come across the sea. Such a flora, however, in its composition shows its accidental character. On the other hand, the example of "Gottska Sandœ," in the Baltic, a small island situated less than 20 miles (37 kilometers) from the large island of Gotland and 50 miles (93 km.) from the mainland of Sweden, a moraine bank emerged from the sea during the *Littorina* epoch of postglacial times, shows that complete plant associations may be transported over the sea. Sernander (Skandinaviska Vegetationens Spridningsbiologi, Upsala, 1901, p. 407) remarks expressly that "in none of its plant associations are any gaps noticeable in comparison with the corresponding associations on the mainland," but the distances here involved are slight, of course, compared with those between the Færöes and Scotland or between the latter and Norway. With regard to the Færöes it is difficult to believe that so complete a representation of the Scotch flora could have crossed a sea about 170 mile (315 km.) wide, the distance from Scotland at the present level of the sea. If we assume, however, that the Færöes were connected with Scotland during the maximum glaciation, and that this connection afterwards ceased through a gradual submergence, it is evident that the distance between land and land for a considerable time cannot have been much more than 60 miles (111 km.). The conditions under such circumstances must have been favorable enough to have allowed the immigration of the temperate Atlantic species to which such a distance would not be prohibitive. This suggestion would explain the whole of the Færöe situation, and I hope further on to show that it is the probable solution.

Applying the above to the question of the invasion of the west Norway biota we conclude that the so-called Atlantic and Arctatlantic flora there cannot have crossed the North Sea as it is now limited. On the other hand, I am not prepared to deny the *possibility* of the whole assembly having crossed the 40 miles (74 km.) of the Norwegian channel, though I confess that I have my doubts whether such plants as the 27 species of Atlantic hepaticæ could have been transported that distance over the sea. But the most important

conclusion is, that if the terrestrial fauna can be shown to have come that way, the plants fully sustain the whole theory of a land bridge. The plants in that case more particularly prove the direction whence came the invasion, while the animals demonstrate, in addition, that there must have been a land bridge in that direction.

Not all terrestrial animals,[1] however, are equally suitable to prove such connection. Obviously, birds are of less use than plants. Their general distribution, such as that of the ptarmigan, the twite, and the rock pipit, may show the direction whence they came, but even the ptarmigan would be able to cross the Norwegian channel, though it is very doubtful if it could cross the North Sea at the present level of the sea. I am, therefore, not going into detail here about cases such as those of the west Norway wren (*Anorthura bergensis*) and the chickadee (*Parus colletti*) although they fit very well into the general scheme. I have on another occasion (SMITHSON. MISC. COLL. (Quart.), XLVII, 1905, pp. 428–429) called attention to the case of the dipper (*Cinclus*), and shall here only mention *Columba livia,* the rock pigeon, as another bird which probably reached west Norway from Scotland.

The insects also will have to be left out of consideration, though it should be mentioned that an element of the west Norwegian insect

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[1] The present essay deals only with the terrestrial biota, but if a Scoto-Norwegian land bridge ever existed, as here suggested, a littoral fauna and flora must have accompanied the dispersal of the terrestrial one. To prove in detail the existence of such a littoral assemblage would add a very important link to the chain of evidence, but various reasons prevent its elaboration by me. The case of a characteristic littoral fish may serve as an example in this connection, however.

The *Blennius* (*Lipophrys*) *pholis,* or shanny, is one of the most characteristic beach animals. According to Day (Fish. Great Brit. Irel., I, 1884, p. 204) it "is found in rock pools accessible at low water and does not appear to frequent deeper localities." Smitt (Scand. Fishes, 2d ed., I, 1892, p. 216) says that it "prefers to live above low-water mark and seems . . . to find pleasure in being left dry at ebb-tide." The female deposits its eggs in "a small hole with a narrow entrance just above low-water mark." Its geographical distribution is characteristically "Atlantic." "Its true home is on the coasts of Great Britain and Ireland, extending southward . . . into the Mediterranean at least as far as Barcelona" (Smitt, p. 217). According to Day (p. 205) it "appears to be distributed almost everywhere in pools between tide marks around the British coast. . . . In Ireland it is common." It is not found in Denmark or Sweden, but in Norway it occurs on the west coast from Stavanger northward at least up to Manger, a little north of Bergen.

fauna corresponds exactly to the Atlantic group of plants, as shown by Sparre Schneider.[1]

The terrestrial isopods seem to possess means of rapid dispersal, and many of them probably owe their present wide range to the agency of man. An exception is apparently furnished by *Ligyda* (=*Ligia*) *occanica* (Linnæus) which lives near the water's edge on exposed saltwater beaches. "Along the western coast of Norway this form" according to Sars (Acc. Crust. Norway, II, 1899, p. 157) "occurs rather plentifully and extends northwards at least to the Trondhjem Fjord," while outside of Norway it is found on the coasts of "Denmark, Prussia, Belgium, France, Spain, Britain, Færœ Islands." It is consequently an eminently "Atlantic" species, and there can be but little doubt that it has come to west Norway from Scotland. It can hardly be said to prove a land connection at any time, however, since it appears probable that it might be easily caried across salt water by currents for such a distance as the width of the Norwegian channel, though it is uncertain whether it could cross the North Sea at its present level.

The earthworms might furnish excellent tests for the presence of a land bridge, were their distribution known in greater detail and were we assured that they are not introduced recently by man. All the species thus far recorded from Norway[2] belong to the group which Michaelsen characterizes as "Weitwanderer," with the exception of an indigenous species, *Helodrilus* (*Bimastus*) *norvegicus,* which has been found in Suldal, Nordreisen, and Tromsœ. Michaelsen, however, regards it as a form of comparatively recent origin and doubtfully distinct specifically from *H.* (*B.*) *constrictus* which also occurs there. Of the thirteen species recorded by him from Norway nine occur about Kristiania and Drammen in the eastern part of the country, while four are reported from the western and northern coast only. Of these *Helodrilus* (*Allolobophora*) *longus* has only been found at Stavanger and may, therefore, be a recent

[1] Coleoptera og Lepidoptera ved Bergen og i nærmeste omegn (*Bergens Mus. Aarb.,* 1901, No. 1). On pp. 20–21 he enumerates 31 "Atlantic" coleoptera, 4 hemiptera, and 23 lepidoptera. On p. 9 he calls attention to the British bumblebee, *Bombus smittianus,* which also occurs along the extreme western coast of Norway from Jæderen to Lurœ in Nordland (66½° north lat.), and on p. 161 to the noctuid moth, *Aporophyla nigra,* which occurring at Bergen, but not in Denmark, Sweden, or Finland, furnishes among the lepidoptera "one of the most important proofs of the originally close connection between the British Islands and southwestern Norway."

[2] W. Michaelsen, Die Lumbriciden-Fauna Norwegens und ihre Beziehungen, in *Verh. Naturw. Ver. Hamburg* (3), IX, 1902, pp. 1–13.

introduction. The northern record of the three others, viz., *H.* (*Dendrobæna*) *rubidus* (*typicus*), *H.* (*B.*) *norvegicus* and *H.* (*B.*) *constrictus,* is very dubious, in as much as it uncertain which of them, if more than one, occurs on Lavangsfjell in Tromsœ Amt, and in Lofoten. However, as *H. rubidus* and *H. constrictus* belong to the most widely distributed species, their absence about Kristiania as well as in south and central Sweden, while occurring in Suldal, Stavanger and Bergen, in western Norway, is highly suggestive. The presence of one of these three in the province of Tromsœ and in the Lofoten Islands, and, last but not least, the fact that one of them has had time to differentiate into a separable form, make it pretty certain that we have not to do with species introduced by man. Add to this the occurrence of *H. constrictus* in Britain and *H. rubidus* in Iceland, and we have a distribution tallying very well with that of the other "Atlantic" species. Considered by itself the case of these earthworms cannot as yet be taken as conclusive evidence in favor of a Scoto-Norwegian land bridge, because of the many uncertainties involved, but in connection with the rest of the biota it assumes enough significance to justify our calling attention to it.

The land and fresh-water molluscs might also possibly furnish valuable data if their identity and distribution in west Norway were better known, especially as compared with the Scotch forms. Attention is here only directed to *Helix* (*Tachea*) *nemoralis* which according to Miss Esmark (*Journ. Conchol.,* v, October, 1886, p. 108) is "only found on the west coast" of Norway, from Bergen to Stavanger. The species, it is true, is common in Denmark and rather common in the extreme southern province of Sweden, but becomes rare northwards, only reaching Göteborg on the west coast of Sweden and Jemtland on the eastern side.[1] It will be seen, however, that the two habitats on the Scandinavian peninsula are widely separated. The distribution in the south and east shows the species to have arrived there from central Europe over the Baltic land bridge, while its characteristic "Atlantic" distribution in west Norway distinctly points to a land connection with the British Islands where it is widely distributed both in Scotland and Ireland.

Under other circumstances the most convincing tests for uninterrupted land connections are furnished by batrachians and fresh-water fishes. Unfortunately they are very slow travelers, especially the latter. The absence of evidence of any of them having crossed

[1] Westerlund, Synopsis Molluscorum Extramarinorum Scandinaviæ, in *Acta Soc. Fauna Flora Fennica,* XIII, No. 7, 1897, pp. 56–57.

the supposed Scoto-Norwegian land bridge is, therefore, no proof against its former existence, but may only show that the land connections we are considering in this paper only lasted a comparatively short time.[1] Most convincing evidence of this is furnished by the fact that while the characteristically "Atlantic" species are found both in Ireland and west Norway, though more numerous in the former than in the latter, neither has more than two species of tailless batrachians, viz., one frog and one toad, the frog belonging to the same species, *Rana temporaria,* the toad, however, to two distinct species, *Bufo bufo,* in west Norway, and *Bufo calamita* in southwest Ireland. Scotland and west Norway have also only two species in common, viz., *Rana temporaria* and *Bufo bufo,* and these might, therefore, have been suspected of having come to the latter country from the west, were it not that they are absent in the islands north of Scotland. The absence of *Bufo bufo* in Ireland is also against such an assumption, since it is probable that the connection between Ireland and Scotland was severed *after* the supposed connection between Scotland and west Norway had been broken. Both species, moreover, are widely distributed over the whole northern portion of the palearctic region from the Pacific to the Atlantic without any special western tendencies. Both probably entered Scandinavia from the south. West Norway is particularly poor in fresh-water fishes, the only land-locked species being the charr (*Salvelinus alpinus*), but as it frequents salt water in subarctic climates it is useless for our purpose.

These groups of animals failing us, we have to fall back upon the mammals as furnishing the second best test of a continuous land connection. Of course, if the terrestrial species which we have discussed above (pp. 462–480) came to west Norway from the west, there must have been at least a very close approximation of the two land areas. The red deer is a good swimmer and is able to cross

[1] That such a period, although "comparatively short," may represent a quite respectable space of time will be seen from the following consideration: Brögger (Strandl. Beligg. Sydœst. Norge, 1905, p. 290), estimates the time which in southeastern Norway has lapsed since the maximum of the postglacial submergence at 18,600 years. It is pretty certain that all the fresh-water fishes of eastern and southern Norway have immigrated since then into those parts of the country from southern Sweden. The climatic conditions may not at first have been favorable, but during the last 10,000 to 14,000 years they probably offered no obstacles. Nevertheless, not one of them has as yet reached the waters of west Norway. The much longer Scoto-Norwegian land bridge may, therefore, easily have lasted at least 10,000 years without any fresh-water fishes having been able to cross it.

fjords and sounds several miles wide, but it is not credible that it could have crossed the 40 miles of the Norwegian channel, if the latter had been formed and was always free of ice during the period in question. I have shown elsewhere, however, that this channel, if existing at the time, probably was frozen over in winter. But the smaller mammals cannot well be assumed to have wandered such a distance across the ice, and we are therefore compelled to conclude that the land connection was complete and uninterrupted at the time of this invasion.

We have thus come to the result that a composite biota, consisting of numerous cryptogamous and phanerogamous plants with a full complement of terrestrial animals during some period of glacial times subsequent to the megaglacial climax invaded western Norway between 59° and 63° north latitude from Scotland over a continuous land bridge which did not stay uninterrupted long enough to allow the slow traveling species, among them the batrachians and fresh-water fishes, to pass over.

VIII. The "Subatlantic" Biota

Before concluding the biogeographical considerations involved it is desirable to refer briefly to the plants and animals more or less characteristic of the southern coast of Norway between Stavanger and Arendal, which following Blytt's example have been termed the *Subatlantic* biota. At the western extremity of their distribution in Norway they meet the southern members of the Atlantic biota, their boundaries frequently overlapping. With a few of the more widely distributed species it is therefore sometimes difficult to decide to which of the two groups they properly belong. One of these is the holly (*Ilex aquifolium*), for which reason I have entirely discarded the term "Ilex-flora" as being ambiguous and confusing.

A characteristic feature of the distribution of these Subatlantic plants is that they occur in Denmark, separated from Norway by the 60 miles (111 km.) wide arm of the North Sea known as Skagerak. In Britain and in Ireland some are wanting and the distribution of others is decidedly southern.

We have seen above that Blytt and others regarded them as having invaded southern Norway from the south (p. 460) while other botanists maintain that they slowly crept along the west coast of Sweden into Norway. Many distributional facts, especially the lack of many of the species, living or fossil, in the intervening country, militate against the latter theory, and after Sernander has

shown that a channel as wide as the Skagerak is capable of being crossed by a numerous flora there is no necessity for assuming the more roundabout route.

On the other hand, there is no evidence to show that a terrestrial fauna has invaded Norway from that direction. It is pretty nearly conclusive evidence that none of the mammals assigned to the Scoto-Norwegian invasion have been found fossil in Denmark. True, both reindeer and red deer have been found there, but an inspection of Winge's photographs (*Vid. Med. Naturh. For. Kjöbenhavn*, 1904, pls. VII, XI) of specimens in the Copenhagen Zoological Museum shows that they belong to forms different from those inhabiting Norway. Of the red deer Winge (p. 262) indicates two different types in Denmark, one confined to the islands, the other occurring alone in the Jutland peninsula, but also occasionally in the islands. A comparison of Lönnberg's fig. 1 (*Ark. Zool.*, III, 1906, p. 4) with Winge's pl. VII, fig. 2, suggests the identity of the Danish fossil island form with the red deer of south Sweden, the typical *Cervus elaphus*, while the Jutland form may well be the same as one of the continental European races which Lönnberg terms *Cervus elaphus germanicus* (Desmarest). So much appears certain, however, that none of the Danish red deer have anything to do with the Scoto-Norwegian *Cervus atlanticus*.

It seems then fairly well established that while southern Norway has received part of its flora and fauna from the south during post-glacial times, as distinguished from the biota which entered from the southeast, there was no direct land connection between Denmark and Norway during that period.

IX. A Sketch of the Geological Considerations Involved

I have now arrived at the point hinted at in the introduction to this paper (p. 459) where it becomes incumbent upon me "to show that my theories are not inconsistent with accepted principles and with the general outline of conservative geological opinion," and I hope to be able to do so in the following pages.

That a Scoto-Norwegian land bridge is not the mere fantastic vaporings of a biogeographer with a theory to prove, can be shown by numerous quotations from the writings of prominent geologists and physiographers. Thus professor J. W. Judd, in his presidential address to the Section of Geology of the British Association (Rep. Brit. Ass. Adv. Sci. Aberdeen Meet., 1885, p. 1001) has the following to say:

"The early history of Scotland is inextricably interwoven with that of Scandinavia. . . . To us the separation of Scotland and Scandinavia is an event of very recent date indeed; it is not only an accident, but an uncompleted accident! The Scottish Highlands, with the Hebrides and Donegal on the one hand, with Orkney and Shetland on the other, must be regarded—to use a technical phrase—as mere 'outliers' of the Scandinavian peninsula."

Dr. Hans Reusch, the distinguished director of the Geological Survey of Norway, in 1888 (Bömmelöen og Karmöen, p. 420), concludes that "the Scandinavian mountains assuredly constitute with the mountains in the northern part of the British Islands *a single system* only interrupted by the subsidence of the area of the German Ocean," or North Sea. Suess (Antl. Erde, II, 1888, p. 100; Face Terre, II, 1900, p. 125) endorses these views and states that Shetland, the Orkneys, the Scotch Highlands, a large portion of Ireland and Wales "are to be regarded as the continuation of the folded mountains in Norway. The sea which separates Scotland from Norway, as shown by the enormous faults of the Scotch coast, lies over a sunken portion of this mountain system . . . the *Caledonian Mountains.*"

The hydrographers have come to similar results. The latest, most thorough, and most detailed study of the problem is by Professor Fridtjof Nansen (Norweg. North Pol. Exped., IV, No. 3, 1904), who in reviewing the history of the formation of the Norwegian continental shelf concludes (p. 166) that it "has comparatively recently been elevated, at least 300 m. ['or probably more' p. 189] higher than now, when the level of the barriers of the great submarine fjords was developed." As to the time he adds on p. 167: "To judge from the similarity between the continental shelves of Norway, the Færöes and Iceland, it seems probable that the shelf is, at least to a great extent, postmiocene, *i. e.,* pliocene and pleistocene."

This suggestion as to the time of the land bridge is fully borne out by the investigations of Peach and Horne regarding the glacial phenomena of Shetland and Orkney, which point to "the conclusion that they were glaciated by land ice that moved from the North Sea towards the Atlantic" and "that the ice must have moved westwards across the submerged platform of which Shetland and Orkney are the surviving relics" (Rep. Brit. Ass. Adv. Sci. Aberdeen Meet., 1885, pp. 1036–1077). Professor Judd, in the presidential address alluded to above is even more definite as to the time, as follows (p. 1008):

"Down to postglacial times Scotland, and what are now its outlying islands remained united with Scandinavia. I need not remind you how, during the glacial period, they were the scene of a similar succession of events; while from their then far more elevated mountain-summits streams of glacier-ice flowed down and relieved the mantle of snow which enveloped them.

"But at a very recent geological period, and indeed since the appearance of man in this part of our globe, the separation of the two areas, so long united, was brought about. In the district now constituting the North Sea, which separates the two countries, great faults, originating in the Tertiary epoch, appear to have let down wide tracts of the softer secondary strata among the harder crystalline rock-masses. The numerous changes of level, of which we find such abundant evidence around the shores of this sea, facilitated the wearing away of the whole of the softer secondary deposits, except the slight fringes that remain along the shores of Sutherland, Ross and Cromarty, on the one hand, and the isolated patches forming Scania, Jutland, and the surrounding islands on the other. Little could the Vikings, as they sailed over this shallow sea, have imagined that their predecessors in these regions were able to roam on foot from Norroway to Suderey!"

These quotations might be added to *ad libitum* and, as hinted at in my introductory remarks, I might make my task easy by simply showing that eminent geologists have advocated the existence of a Scoto-Norwegian land bridge in postglacial times, that is, *after* the disappearance of the neoglacial ice sheet. If it were generally accepted, if it could be termed "an established geological fact" that the distribution of land and water in northern Europe "*after* the epoch of the last great Baltic glacier" was as represented in Geikie's map (Great Ice Age, 3 ed., 1894, pl. XII) there would probably be very little opposition to my theory of the Scotch origin of the characteristic biota of west Norway. Unfortunately, a postglacial connection meets with disapproval of geologists equally distinguished. It is the latter which I must try to convince that the animals and plants discussed here may have come from the west, or at least I must try to make my case so plausible that they are willing to consider the question in the light of the facts and theories brought together in this paper.

In glancing over the Norwegian geological literature relating to these questions one is struck by the great attention given to the various glacial submersions and the corresponding deficiency with

regard to the elevation of the land during the same periods. The reason is obvious, viz., that on the present surface we have evidence of the former subsidence, while the sea hides the land which once connected islands and continents. Positive proof of these connections, and of their extent in time and space, are therefore much more difficult to produce. The impression left upon the casual student of these phenomena is therefore unavoidably that the glacial epoch was one of subsidence chiefly, consequently it cannot be too strongly emphasized, that while this is true to a great extent with regard to the later phases of the glacial time, it is not true of the early and middle stages.

That there is ample proof of western Norway having had an altitude of *at least* 180 meters higher than now since the megaglacial stage is conclusively shown by no less authority than Professor W. C. Brögger.[1] The accumulations of littoral species of shells on the banks off the west coast of Norway at depths down to 180 meters or more demonstrate a corresponding elevation which, according to him, existed immediately before and possibly during the early stages of the second (Scandinavian) glaciation. He synchronizes this elevation with the one demonstrated by Judd and others from the Rockall bank, and by Jensen from the Færöes, both of which indicate elevations of at least 180 meters: "The entire material of observations anent these sunken littoral banks, with a fauna partly to a greater extent arctic, partly mixed, and partly southern, thus points to an extensive elevation of the sea bottom from Iceland, the Færöes, Rockall, Scotland, the Shetland Islands to the Norwegian coast during the last interglacial period" (p. 107). It should be noted, however, that both the reports of the Rockall expedition and of A. S. Jensen refer this elevation to the postglacial period, that is, to the time *following* the neoglaciation (second Scandinavian glaciation). This question, therefore, appears to the biographer as being still open, and it is so regarded in the following considerations.

The most superficial study of the phenomena of the glacial epoch demonstrates that there were great changes of level, and more elaborate research establishes the fact that these changes not only vary locally in intensity, but that the rise and fall of the sea-level is not synchronous over the whole area affected. I need only mention what Knipowitsch says on the last page of his monumental "Grundzüge der Hydrologie des Europäischen Eismeeres (*Zap.*

[1] Om de Senglaciale og Postglaciale Nivaaforandringer i Kristianiafeltet, in Norges Geol. Undersög., No. 31, 1900, pp. 100–111.

Imp. Russk. Geog. Obstch., XLII, 1906, p. 1510): "The depressions and elevations need not at all take place uniformly over large areas. These processes may occur in entirely different ways in the various parts of the same ocean. While one part of the ocean shows great depression or elevation of its floor, another may be affected much less, or not at all, or may even show opposite processes. The unevenness and irregularity of the depressions and elevations may cause a very complicated sequence of the physico-geographical as well as biological changes."

Such diversity does not point to cosmic causes. As a matter of fact, the changes of level are so intimately connected with the various phases of the glacial phenomena that it seems out of the question to regard them as mere coincidences.[1]

Of the various theories which have been propounded to account for the uneven submergence and elevation of the land masses, the one which attributes the depression to the weight of the accumulated ice and the elevation to the unloading of the enormous weight by melting under different climatic conditions, seems to meet most of the requirements which can be put to it. This hypothesis is based upon the theory of the elasticity of the earth's crust, the necessary consequence of which is, that if the crust be depressed in some places, it must rise correspondingly elsewhere, while between these areas there must be a nodal axis, or line, which is practically stable, where no motion of any consequence takes place. The elasticity of the crust furthermore requires a return movement following the removal of the depressing agency, a rebound which does

[1] The very magnitude of the glacial phenomenon in connection with its diversity suggests that it is not due to a single cause but to a concurrence of many factors. It may be easy enough to reduce *ad absurdum* every one of the various theories which would account for the whole phenomenon by the assumption of a single cause, but it seems possible that a combination of the various theories, meteorological, geographical, and astronomical may be effected in such a way as to frame a plausible working hypothesis. If all the different causes functioned together towards the same end, it would not be necessary to work each of them to its extreme, and, therefore, often absurd, limit. It might then be unnecessary to move the north pole so very far out of its place as would be required if a change of the earth's axis were regarded as the whole solution of the question, nor would it be necessary to assume such extreme changes of level as 1,000 to 2,500 sea-meters, if the height of the land were alone to account for the fall of temperature. Neither would it then be imperative to postulate that an unbroken land bridge between Scotland and Greenland absolutely shut off the Arctic Ocean from the Atlantic, nor to lower to any very great degree either the temperature or the volume of the Gulf Stream.

not cease on reaching the former level of equilibrium but continues proportionally to the amount of the original pressure. A reciprocal motion is thus set up in the earth's crust, the oscillations of which gradually become smaller and smaller.[1]

Among the many complications which would arise from a considerable change of level in the North Atlantic one of the most important would undoubtedly be the interference with the poleward transmission of warm water, a phenomenon for which we retain the convenient name of the Gulf Stream. A deflection of this flow, which should materially diminish the amount of the warmer water passing into that part of the north Atlantic Ocean lying north and east of a line between Scotland and Iceland might unquestionably bring about changes in the atmospheric conditions which would be both considerable and far-reaching, producing ice-age conditions there and in the countries adjacent.

Taking this for granted and starting from this as our fundamental axiom we may then imagine the following sequence of events in the region we have discussed.

Biologists as well as geologists are now fairly well agreed that the latter part of the Tertiary was characterized by a general elevation of the land considerably higher than now,[2] the result of a gradual rise.

In our region the rise continued until reaching the 600 sea-meter[3] level, thus shutting off the Gulf Stream from the North Atlantic by a land bridge connecting Scotland with the Færöes and Iceland though probably not extending to Greenland. The combination of such a great elevation, the cold due to the deflection of the warm current, and the increased volume of the cold Greenland current produced atmospheric changes resulting in the glaciation which gave Norway

[1] See N. O. Holst, Bidrag til Kännedomen om Östersjöns och Bottniska Vikens Postglaciala Geologi, in *Sveriges Geol. Unders.*, Ser. C, No. 180, 1899, pp. 113–128, especially p. 127.

[2] Say, on an average, 200 meters. See H. F. Osborn's map, *Science* (n. s.), XI, April 13, 1900, p. 564.

[3] The abolition of the old units of fathom and foot for the meter often results in obscurity or awkwardness in discussions of this kind, in as much as it is nearly always necessary to state whether the figures signify depths below the present sea level or heights above it. To avoid much confusion I have, therefore, employed the terms sea-meter and land-meter for the relative depth and height in question. Thus when I say that the land was raised 100 sea-meters, I mean that the sea-level was lowered 100 meters below its present stand, and when I say that the land was depressed 100 land-meters I mean that sea-level then was 100 meters higher than at present.

HYPSOGRAPHIC MAP OF NORTHWESTERN EUROPE AND ADJACENT SEAS. FROM SVENSKA HYDROGRAFISK-BIOLOGISKA KOMMISSIONENS SKRIFTER

a climate and ice conditions like Greenland and allowed glaciers from Scandinavia to descend upon Shetland and Scotland across the land now occupied by the North Sea. When the ice-cap had reached its maximum its weight counteracted the force causing the upward movement of the earth's crust, and finally overcoming it effected a downward movement. The rate of depression was probably not so great in our region as further east and south. It must be remembered that western Norway and Scotland were on the periphery of the ice-cap, the apex and greatest mass of which was considerably to the eastward. Suppose that this uneven depression resulted in such a tilting that the sea-level in the west of Norway and Scotland stood at the present 200 sea-meter curve, while to the east and south of Scandinavia it had already reached the present 200 land-meter level. At this stage in the west we would have western Norway still united with Scotland and Ireland,[1] but elevated only 200 meters more than now. The northeastward flow of the warmer Atlantic water would consequently have resumed its normal course long ago through the Færöe Channel, and the climate would be considerably ameliorated, especially along the extreme southwestern coast-line.[2] To the east and south of Scandinavia, as we have supposed above, the land was depressed at least 100 and possibly 200 sea-meters. But this depression meant the melting off of the peripheral eastern part of the ice-cap and the transgression of the Arctic Ocean over parts of northern Russia and northern Germany in its place, with an Arctic current coming down along the eastern base of Scandinavia, a veritable Hudson Bay with a corresponding climate. Scandinavia united in the west with Scotland and Ireland formed then an elongated narrow island, the western and northern coast of which were washed by the warm Atlantic waters, the eastern and southern by the Arctic cold current. While previously the ice-cap had been melting due to the relative subsidence and the resumption of the Gulf Stream, the arrival of the Arctic Sea on the east side would cause an increase of precipitation. The result would be a recrudescence of the glaciation and a notable acceleration of the depression, a stage corresponding to the second, or Baltic, glaciation of most Scandinavian geologists, the neoglaciation of Hansen.

[1] Something like Scharff's map, Hist. Europ. Fauna, 1899, p. 126.

[2] The hardier portion of the Færöe flora may have reached these islands before the channel had been reopened, while the temperate species followed later, as suggested on p. 491.

Scharff's "Arctic" migration and the red deer (as well as man) had already reached Scotland from central Europe by this time, when the road behind them was shut off. From here they invaded Ireland and later Norway.

Assuming that it has been made to appear probable that the "Atlantic" element of the west Norway biota invaded that country from Scotland, there is yet another question which must be considered, viz., did these plants and animals come simultaneously, or do they belong to two different invasions? Many of the plants require rather diverse climatic conditions, and so do some of the animals. Assuredly, the red deer and the lemming do not belong to the same life zone! Nevertheless, there does not seem to be any good reason why the land bridge in question could not have presented climatal conditions sufficiently different for the two (adjacent) life zones. We have presupposed a warm current laving its western shore and a more or less cold sea limiting it on the east, thus creating conditions extreme enough for our purpose. Of course, if there were two separate land connections, one before and the other after the neoglacial maximum, the problem of the two life zones would be correspondingly simplified.

It should be clearly understood that by avoiding the term "interglacial" in the discussion of the existence of a Scoto-Norwegian land bridge since the megaglacial maximum I have tried to keep out of any controversy over the question whether there were more than one glacial period in Scandinavia. As far as west Norway is concerned it appears to me that the probability is against two separate and distinct glaciations interrupted by a long period of mild climatic conditions. From the character of the animals and plants whose occurrence in western Norway I am attributing to an invasion following the megaglacial maximum and preceding that of the neoglacial stage, the conclusion may be drawn that the climate, even along the west coast of the land bridge, was not milder than that of the present time, but that, on the whole, it had a more continental character owing to the greater land area to the west. With the depression of the land, from having stood so high as to shut off the Gulf Stream, to a level of say 200 sea-meters, and the consequent reappearance of that temperating agency, an amelioration of the climate must have taken place, but while the glaciers retreated somewhat into the interior, it does not seem likely that they left the coast altogether. At the Norwegian end of the land bridge we may perhaps have had conditions similar to those of Norway under the Arctic circle or like those in the Mt. Elias region of Alaska at the present time, while from the interior vast glaciers, much larger than Justedalsbræ or Folgefonn to-day, sent occasional arms to the sea. The neoglacial increase there may then be regarded only as a recrud-

escence of glacial activity, a mere hump on the downward curve of the general decline from the megaglacial apex. It may have been due not so much to a lowering of temperature as to additional precipitation caused by the increase of the area of the sea to the east as the land sank more rapidly and deeper in that direction. If such be the case, it may only cause confusion to apply the term "interglacial"[1] to this particular stage which may not be synchronous with similar, but more protracted and better differentiated intervals elsewhere.[2] There are certain indications that the phenomena of rise and fall, severe and mild climatic conditions, along the northwestern periphery and those in the south and east, so far from being simultaneous, may have been alternating.

This reservation is necessary since the land bridge alluded to above corresponds to the stage hinted at as "interglacial" by Brögger (Norges Geol. Undersög., No. 31, 1900, p. 105; Norge i 19 Aarhundr. I, 1900, p. 23) by Hansen (Landn. Norge, 1904, p. 281 seqv.), and by Wille (*Nyt Mag. Naturv.* XLIII, 1905, p. 332). Whether the Scotch invasion can be assumed to have taken place during this period and the animals and plants survived the neoglaciation depends, of course, on whether the climate during the latter can be supposed to have been temperate enough for all the species, a question to be discussed further on (p. 510). I myself am inclined to the opinion that it was, and that the whole biota continued its existence in western and northwestern Norway throughout the neoglacial stage, but I admit that there is a possibility of a reëstablishment of the land bridge in postglacial times. The following considerations explain the train of reasoning upon which such a possibility appears plausible.

After the ice of the second glaciation began to melt off, the unburdened land started to rise again. The Swedish geologists have shown that in eastern and southern Sweden this elevation so far from being uniform was interrupted by long periods of repeated and gradually decreasing submergences, the maxima of which show considerable changes of level, thus the *Ancylus* depression reached

[1] If the term be only used according to its original significance to any period between two glacial maxima, there can be no objection to its use, but the common application of it more specifically to layers intercalated between two glacial deposits or moraines renders its use in the present connection inexpedient.

[2] It is worthy of note in connection with the above, that *warm* "interglacial" stages are now being discredited even in Scotland. See J. F. Jamieson, On the Interglacial Question, in *Geol. Mag.* (5), III, December, 1906, pp. 534–536.

" more than 200 m. (?) and the *Littorina* depression about 100 m.,"[1] with a corresponding rise between. In southern Norway, *i. e.*, along the coasts of Skagerak, these oscillations apparently have been comparatively insignificant. Professor W. C. Brögger, in his recent admirable publications on the changes of level in this region[2] sees but doubtful indications of the *Ancylus* depression in Norway (Nivaafor., p. 645) and the *Littorina* depression he finds amounted to only 2 to 3 meters at Kristiania (Strandlin., p. 99), a result which he characterizes as only " a halt or a discontinuance of the rise accompanied by a slight depression." Holmboe[3] and Oeyen[4] have also ascertained a slight depression on Jæderen (8–16 meters) though it appears to me somewhat doubtful if this is absolutely synchronous with the other.

These depressions which in eastern Sweden were so considerable must have had their corresponding rise elsewhere, and as Kristiania, according to the above, was near the nodal axis of the reciprocal movement, it is reasonable to suppose that the rise on the other side of this line must have been correspondingly conspicuous along the west coast of Norway north of 60° north latitude. A maximum rise of 200 sea-meters at the western edge of the coast platform corresponding to and approximately synchronous with the *Ancylus* depression would therefore appear to be within the possibilities. Such a rise[5] would restore the connection with Scotland and furnish easy means for the red deer and the corresponding portion of the Atlantic biota to pass over to west Norway.

It is not to be expected that such a theory will receive the sanction of all the geologists. There is a considerable amount of disagreement among them as to the interpretation of the various phases of the glacial epoch, its climatic and physiographic features. There

[1] N. O. Holst, Bidr. Östersj. Bottn. Vik. Postglac. Geol., 1899, p. 127.

[2] Om de Senglaciale og Postglaciale Nivaaforandringer i Kristianiafeltet (Kristiania, 1900–1901; xii + 732 pp. + xix pls.); Strandliniens Beliggenhed under Stenalderen i det Sydöstlige Norge (Kristiania, 1905; viii + 340 pp. + xiii pls.) (= Norges Geologiske Undersögelse, Nos. 31 and 41).

[3] Jens Holmboe, Planterester i Norske Torvmyrer, in *Kristiania Vidensk. Selsk. Skr.*, 1903, I, No. 2, p. 11.

[4] P. A. Oeyen, Tapes-niveauet paa Jæderen, in *Kristiania Vidensk. Selsk. Skr.*, 1903, I, No. 7, p. 44.

[5] This rise would consequently be represented in the extreme west by Jensen's Færöe banks (in Norges Geol. Unders., No. 31, 1900, pp. 106–107) and by the Rockall bank which Professor T. R. Jones, following Geikie, considers postglacial (Notes on Rockall Island and Bank, in *Trans. Roy. Irish Acad.*, XXXI, pt. iii, 1897, p. 97).

are authorities who recognize up to six different glacial periods, or stages, with corresponding interglacial times, while others refuse to recognize more than one glacial period, denying the existence of an interglacial epoch, and so forth. Probably most of these opposing contentions are more or less reconcilable, if not given too wide an application. Even a glacial climate is not uniform over such a vast territory as is here involved, nor are the heavings of the earth's crust uniform. The whole question is exceedingly complicated, as one set of phenomena may cause diametrically opposite results in different places, because the combination with other important factors is so utterly unlike.

One is forcibly struck by this when considering the results obtained by the geologists who have worked out the Baltic situation in Sweden and the closely related conditions in Denmark and southeastern Norway. But to conclude that the same series of events must have obtained everywhere else is to frame a Procrustes bed upon which scientific truth may suffer. Such reflections naturally present themselves when comparing these results with others, say for instance, with those which the celebrated author of "The Great Ice Age," J. Geikie, has arrived at in Scotland. If we compare his views of the sequence of postglacial events in the latter country with those of the Scandinavian geologists we are at once facing the discrepancy that the latter refer the warmer periods to the times of greatest depression, while with him elevation and mild climate, submergence and cold conditions are coincident. In the latest we have from him on the subject[1] this is very forcefully maintained. It is not difficult to imagine, however, that conditions causing certain climatic changes in the Baltic may have had other results in Scotland, and it is therefore plain that the events such as rise and fall of the land, continental or oceanic climates, etc., in the two areas are not necessarily synchronous. If in Scotland we find a succession consisting of a rise, a depression and a rise again, and we find a similar succession in southern Sweden, there is no *a priori necessity* for considering these movements having occurred simultaneously, they may have taken place alternately, that is, the rise in Scotland may have obtained at the time when the land was sinking

[1] James Geikie, On the So-called "Postglacial Formations" of Scotland, in *Jour. Geol.*, XIV, November–December, 1906, pp. 668–682; succession on pp. 675–676. In an article by Lewis, on "The History of the Scottish Peat Moors and their Relation to the Glacial Period," *Scott. Geogr. Mag.*, XXII, May, 1906, p. 252, Geikie has also a "Succession of the Later Glacial and Interglacial Stages in Scotland."

in Scania, and the rise here may correspond to the fall there. And with the climate as with the earth's movements, there are no *a priori* reasons why it might not be mild on the west coast of Scotland at a time when the temperature was rigorous in the Baltic, and vice versa.

But if this is true of Scotland, it is also true of western and northwestern Norway. This part of the latter country is so much nearer to Scotland than to the Baltic and its geological relation to Scotland so much more intimate than to southeastern Sweden that it is much more probable that the glacial events in west Norway were more nearly coextensive in time and degree with those of Scotland than with those of Sweden. Add to this that both the former countries are subject to much the same conditions influencing the climate and that both formed the extreme western edge of the glaciated area, and we are prepared for similar events on both sides of the northern part of the North Sea.

These considerations harmonize very well with the conclusions to be derived from the gradual diminution of the *Ancylus* and *Littorina* depressions towards western Norway, and it seems therefore justifiable to synchronize the Scotch and west Norway postglacial events and to assume that together the two countries went through the reciprocal movements which hinged along a nodal line (not necessarily, or even probably, a straight line) near Kristiania.

Geikie's Mecklenburgian, or fourth glacial stage, the district moraine stage, is by him identified with the Baltic glacier stage (Ice Age, pl. XI), the second or last glacial period, neoglacial period, etc., of the Scandinavian geologists. This period was characterized in Scotland by a submergence (110 to 135 feet, 33 to 41 meters), arctic climate and a land area of greater extent than now. His map of "Europe after the epoch of the last great Baltic glacier" (Ice Age, pl. XII) shows that at this time he considered Scotland and west Norway to be land-connected. It is probably safe to synchronize this rise in Scotland with the elevation during the second glaciation which Brögger (Norge i det Nittende Aarhundrede, I, 1900, p. 23) alludes to as follows: "During the last glaciation the land has probably again risen at least a couple of hundred meters higher than now. This is demonstrated by the occurrence of beach gravel and beach shells on the fishing banks (Storeggen, etc.) off the [west] coast [of Norway] down to a depth of a couple of hundred meters." He continues (p. 24): "Even at the beginning of the period of the formation of the ras [the large terminal moraines along the south-

eastern coasts of Norway] (the ra period, Baltic ice period) the land cannot have been lower than now, but sank afterwards during their formation continually deeper, possibly to a depth about 90 to 100 meters lower than now (at Moss)." The idea that the Scandinavian inland ice in western Norway did not extend beyond the heads of the fjords during any time of the second glaciation seems to be gaining ground among the Norwegian geologists,[1] and if I am correct in connecting the ice-free border land with Geikie's Forestian Scotland, we have a satisfactory explanation of the milder climate and the survival of the Scoto-Atlantic biota from the previous period.

The depression lasted a very long time in eastern Norway, but finally the land began slowly to rise there as the ice cap of the second glaciation melted away. As a concomitant event Scotland and the Scoto-Norwegian land bridge was submerged, Geikie's Lower Turbarian stage, Scotland sinking to 45 to 50 feet (14 to 15 meters) below present level, and the climate became cold and wet.

In the farther southern and eastern portion of the Scandinavian peninsula another depression then took place, the so-called *Ancylus* depression, followed by another considerable rise, the *Ancylus* rise, during which the Baltic became a lake, the *Ancylus* lake. The climate there became warmer.

In eastern Norway, as we have seen, there is no clear indication of this depression and rise to the east, but the reciprocal movement may well have been manifest in west Norway without having been demonstrated there as yet, for in Scotland there are signs of the reciprocity stages of rise and depression, the Upper Forestian stage with its dry and congenial climate representing the rise more or less synchronous with the *Ancylus* depression, and the Upper Turbarian stage, somewhat cold and wet, representing the depression (25 to 30 feet, 8 to 9 meters) synchronous with the *Ancylus* lake elevation.

The subsequent rise in Scotland must then have begun during the Baltic *Littorina* depression. By this time the gradually decreasing movements resulting from the original pressure of the megaglacial ice-cap had become so feeble that they may have left no trace at the extreme periphery of the area affected.

[1] Even Brögger (Norges Geol. Unders., No. 31, 1900, p. 104) admits that "it is therefore probable that during the last great glaciation at least *portions* of the west coast [of Norway, particularly mouth of the Sognefjord] may have been ice-free."

The question next arises: If the Scoto-Norwegian land bridge only existed before the maximum of the second glaciation, could the animals and plants have survived the latter period on the ice-free coast border along western and northwestern Norway? Hansen (Landnaam i Norge, 1904, p. 288) comes to the conclusion that the yearly temperature at the very edge of the neoglacial time cannot have been more than 6° to 8° C. lower than at present, while farther away from the ice it probably was only 5° to 6° lower.

Of the species composing the biota involved probably none requires a more temperate climate than the red deer, and it is therefore sufficient to inquire into the possibility of this species surviving.

The yearly isotherm of the present habitat of *Cervus atlanticus* in Norway is about +6° C. Consequently the inquiry may be formulated as to whether there is reason to suppose that this deer could have survived, if the yearly temperature of the coast strip during neoglacial time was say 7° C. lower than now, or about —1° C? It is well to bear in mind that the distribution of an animal like the deer is not affected so much by the annual temperature as by that of the six hottest weeks of the year, approximately equaling the temperature of the month of July. The average temperature for July in the present habitat of *Cervus atlanticus* is about +13° C. There are plenty of climates having this July isotherm combined with an annual isotherm of —1° C. Such a climate would of course have a much lower isotherm for January than that of western Norway, which is +1° C. The mean temperature of January in such a climate might fall as low as —8° C. Now, can the deer live in a climate indicated by the latter isotherm, and do we know of any region where a species of *Cervus* related to *C. atlanticus* really exists under such conditions? In reply to these questions it is only necessary to refer to the distribution of the central European forms of *C. elaphus* in eastern Europe and it will be seen that the January isotherm of —8° C. indicates the southern limit of the range rather than the northern. It may be objected that in this case we have to do with an extreme continental climate not likely to have obtained in west Norway even during the neoglacial period. It is not difficult, however, to point out some coast with temperatures essentially agreeing with those indicated above and where a form of red deer flourishes at the present day. Such a territory, for instance, is found along the east shore of the Gulf of Tartary from Vladivostok northwards nearly to the mouth of the Amur (only the January isotherm is considerably *lower* than —8° C.) and here a

deer, *C. luehdorffi,* occurs, which on the Pacific coast plays the same rôle relative to the common central Asiatic ancestral stock of *C. elaphus* as does *C. atlanticus* on the Atlantic coast. That pine, birch, aspen and the other trees which form the forests of the home of the latter also thrive excellently in a climate with a temperature of —1° C. for the year, +13° C. for July, and —8° C. for January, it is scarcely necessary to point out, but it may be emphasized that if the Scoto-Norwegian land bridge existed at the time and in the manner advocated in this paper, then the climate of west Norway must have been considerably more continental than at present.

Finally, the question of the so-called Norwegian Channel, the deep, canyon-like depression, 75 to 100 kilometers wide, skirting the southern and southwestern coast of Norway, calls for a few remarks. At its northern extremity it is slightly deeper than 400 meters; it is shallowest off the mouth of the Hardangerfjord where it is about 275 m., and it is deepest at its eastern end in the Skagerak where it reaches a depth of 700 m. There is as yet no entirely satisfactory explanation of its origin. Probably the most commonly accepted hypothesis is that it was scoured out by an enormous glacier at a time when the sea stood near the 400 sea-meter level. If the west Norwegian glaciers at one time extended to Shetland and Scotland, it must have been previous to the excavation of this channel, as obviously no glacier could cross it at right angles. Somehow, its absolutely unique dimensions and its remarkable curved outline makes one wish for a more convincing theory. The other explanation seems to be, that the surface here has dropped down between an extensive system of faults. In support of this it may be said that the inner deep portions of the channel, the Skagerak, admittedly is such a depressed basin, the settling of which is still in progress as proven by the numerous earthquakes which have their starting point here, the last important one being the great earthquake of October 23, 1904. The fact that the settling still continues would favor the theory that the channel is of recent origin, probably late postglacial, and that therefore the land connection with Scotland and Shetland was uninterrupted by the channel.

There are many obscure points yet to be cleared up and explained, and details respecting the various elevation stages may never be obtained, since they are covered by the sea, but I think I may safely claim to have made it appear probable:

1. That if the characteristic and important portion of the animals and plants of west Norway, called the "Atlantic" biota, invaded that country from Scotland, it came by way of a land bridge connecting northern Scotland with western Norway north of 59° north latitude.

2. That this land bridge existed after the first (Scandinavian) great glaciation.

3. That part of this biota surely survived the second (Scandinavian) glaciation along the west coast of Norway, and that possibly the climate was not too severe for all to survive.

4. That there is a possibility of a reestablishment of the land bridge during the "Upper Forestrian" stage with its congenial, more continental climate, during which the tenderer species may have immigrated, in case it should be proven that they could not have come with the hardier ones.

X. Summary

The biota of west Norway between the parallels of 59° and 63° north latitude is composed of several elements, an important portion of which must have come from Scotland.

Some of the most conspicuous members of this biota are even at the present time confined to this coastal region, while others of somewhat wider distribution clearly point to the same coast as their secondary center of dispersal. Numerous other species not modified specifically, or subspecifically, probably accompanied this peculiar biota, a fact which cannot be proven at present on account of the defective status of our knowledge.

This so-called "Atlantic" and "Arctatlantic" biota consists of a large number of species, among which the following are some of the more conspicuous:

(*a*) The whole floral element, termed the "Atlantic plants" by Blytt, consisting of about 60 species of vascular plants, 27 species of hepaticæ, etc.

(*b*) That portion of the Scandinavian "Arctic" plants designated in this paper as the "Arctatlantic" floral element.

(*c*) A number of terrestrial invertebrate animals such as *Helix* (*Tachea*) *nemoralis,* among molluscs; several species of *Helodrilus,* among the earthworms; *Ligyda oceanica,* among the isopod crustaceans; *Aporophyla nigra,* among the noctuid moths; *Bombus smittianus,* among the bumblebees, and a whole series of "Atlantic" lepidoptera, hemiptera, and coleoptera.

(*d*) A restricted littoral fauna, among the vertebrates represented by the shanny (*Blennius pholis*).

(*e*) A number of non-marine birds, such as the ptarmigan (*Lagopus mutus*), the rock dove (*Columba livia*), the rock pipit (*Anthus petrosus*), the twite (*Cannabina flavirostris*), and possibly the dipper (*Cinclus cinclus*).

(*f*) A number of terrestrial mammals, such as the variable hare (*Lepus timidus*), the lemming (*Lemmus lemmus*), the red-backed field mouse (*Evotomys norvegicus*), the wild reindeer (*Rangifer torandus*), the red deer (*Cervus atlanticus*), and the fjord-horse (*Equus celticus*), either wild or domesticated. To this category must also be added the extinct mammoth (*Elephas primigenius*).

It is contended that the mammalian element of the fauna offers a fairly conclusive proof of a continuous land bridge between northern Scotland and west Norway, and geological considerations have been adduced to establish the probability of the existence of this land bridge during the time between the two phases of the glacial epoch known to the Scandinavian geologists as the first and second glaciations, a stage alluded to by many of them as *the* interglacial period.

I have furthermore attempted to make it appear probable that the climatic conditions in west Norway during the second glaciation were not severe enough to preclude the survival there of this biota, although the possibility of a reestablishment of the land connection with Scotland and a consequent second Scotch invasion during the postglacial stage is not absolutely denied.