Means of Dispersal.

Sir C. Lyell and other authors have ably treated this subject. I can give here only the briefest abstract of the more important facts. Change of climate must have had a powerful influence on migration. A region now impassable to certain organisms from the nature of its climate, might have been a high road for migration, when the climate was different. I shall, however, presently have to discuss this branch of the subject in some detail. Changes of level in the land must also have been highly influential: a narrow isthmus now separates two marine faunas; submerge it, or let it formerly have been submerged, and the two faunas will now blend together, or may formerly have blended. Where the sea now extends, land may at a former period have connected islands or possibly even continents together, and thus have allowed terrestrial productions to pass from one to the other. No geologist disputes that great mutations of level have occurred within the period of existing organisms. Edward Forbes insisted that all the islands in the Atlantic must have been recently connected with Europe or Africa, and Europe likewise with America. Other authors have thus hypothetically bridged over every ocean, and united almost every island with some mainland. If, indeed, the arguments used by Forbes are to be trusted, it must be admitted that scarcely a single island exists which has not recently been united to some continent. This view cuts the Gordian knot of the dispersal of the same species to the most distant points, and removes many a difficulty; but to the best of my judgment we are not authorized in admitting such enormous geographical changes within the period of existing species. It seems to me that we have abundant evidence of great oscillations in the level of the land or sea; but not of such vast changes in the position and extension of our continents, as to have united them within the recent period to each other and to the several intervening oceanic islands. I freely admit the former existence of many islands, now buried beneath the sea, which may have served as halting-places for plants and for many animals during their migration. In the coral-producing oceans such sunken islands are now marked by rings of coral or atolls standing over them. Whenever it is fully admitted, as it will some day be, that each species has proceeded from a single birthplace, and when in the course of time we know something definite about the means of distribution, we shall be enabled to speculate with security on the former extension of the land. But I do not believe that it will ever be proved that within the recent period most of our continents which now stand quite separate, have been continuously, or almost continuously united with each other, and with the many existing oceanic islands. Several facts in distribution,— such as the great difference in the marine faunas on the opposite sides of almost every continent,— the close relation of the tertiary inhabitants of several lands and even seas to their present inhabitants — the degree of affinity between the mammals inhabiting islands with those of the nearest continent, being in part determined (as we shall hereafter see) by the depth of the intervening ocean,— these and other such facts are opposed to the admission of such prodigious geographical revolutions within the recent period, as are necessary on the view advanced by Forbes and admitted by his followers. The nature and relative proportions of the inhabitants of oceanic islands are likewise opposed to the belief of their former continuity of continents. Nor does the almost universally volcanic composition of such islands favour the admission that they are the wrecks of sunken continents;— if they had originally existed as continental mountain ranges, some at least of the islands would have been formed, like other mountain summits, of granite, metamorphic schists, old fossiliferous and other rocks, instead of consisting of mere piles of volcanic matter.

I must now say a few words on what are called accidental means, but which more properly should be called occasional means of distribution. I shall here confine myself to plants. In botanical works, this or that plant is often stated to be ill adapted for wide dissemination; but the greater or less facilities for

transport across the sea may be said to be almost wholly unknown. Until I tried, with Mr. Berkeley's aid, a few experiments, it was not even known how far seeds could resist the injurious action of sea-water. To my surprise I found that out of eighty-seven kinds, sixty-four germinated after an immersion of twenty-eight days, and a few survived an immersion of 137 days. It deserves notice that certain orders were far more injured than others: nine Leguminosæ were tried, and, with one exception, they resisted the salt-water badly; seven species of the allied orders, Hydrophyllaceæ and Polemoniaceæ, were all killed by a month's immersion. For convenience sake I chiefly tried small seeds without the capsules or fruit; and as all of these sank in a few days, they could not have been floated across wide spaces of the sea, whether or not they were injured by salt water. Afterwards I tried some larger fruits, capsules, &c., and some of these floated for a long time. It is well known what a difference there is in the buoyancy of green and seasoned timber; and it occurred to me that floods would often wash into the sea dried plants or branches with seed-capsules or fruit attached to them. Hence I was led to dry the stems and branches of ninety-four plants with ripe fruit, and to place them on sea-water. The majority sank quickly, but some which, whilst green, floated for a very short time, when dried floated much longer; for instance, ripe hazel-nuts sank immediately, but when dried they floated for ninety days, and afterwards when planted germinated; an asparagus plant with ripe berries floated for twenty-three days, when dried it floated for eighty-five days, and the seeds afterwards germinated: the ripe seeds of Helosciadium sank in two days, when dried they floated for above ninety days, and afterwards germinated. Altogether, out of the ninety-four dried plants, eighteen floated for above twenty-eight days; and some of the eighteen floated for a very much longer period. So that as $\frac{64}{87}$ kinds of seeds germinated after an immersion of twenty-eight days; and as $\frac{18}{94}$ distinct species with ripe fruit (but not all the same species as in the foregoing experiment) floated, after being dried, for above 28 days, we may conclude, as far as anything can be inferred from these scanty facts, that the seeds of $\frac{14}{100}$ kinds of plants of any country might be floated by sea-currents during 28 days, and would retain their power of germination. In Johnston's Physical Atlas, the average rate of the several Atlantic currents is thirty-three miles per diem (some currents running at the rate of sixty miles per diem); on this average, the seeds of $\frac{14}{100}$ plants belonging to one country might be floated across 924 miles of sea to another country; and when stranded, if blown by an inland gale to a favourable spot, would germinate.

Subsequently to my experiments, M. Martens tried similar ones, but in a much better manner, for he placed the seeds in a box in the actual sea, so that they were alternately wet and exposed to the air like really floating plants. He tried 98 seeds, mostly different from mine, but he chose many large fruits, and likewise seeds, from plants which live near the sea; and this would have favoured both the average length of their flotation and their resistance to the injurious action of the salt-water. On the other hand, he did not previously dry the plants or branches with the fruit; and this, as we have seen, would have caused some of them to have floated much longer. The result was that $\frac{18}{98}$ of his seeds of different kinds floated for forty-two days, and were then capable of germination. But I do not doubt that plants exposed to the waves would float for a less time than those protected from violent movement as in our experiments. Therefore, it would perhaps be safer to assume that the seeds of about $\frac{10}{100}$ plants of a flora, after having been dried, could be floated across a space of sea 900 miles in width, and would then germinate. The fact of the larger fruits often floating longer than the small, is interesting; as plants with large seeds or fruit which, as Alph. de Candolle has shown, generally have restricted ranges, could hardly be transported by any other means.

Seeds may be occasionally transported in another manner. Drift timber is thrown up on most islands, even on those in the midst of the widest oceans; and the natives of the coral islands in the Pacific procure stones for their tools, solely from the roots of drifted trees, these stones being a valuable royal tax. I find that when irregularly shaped stones are embedded in the roots of trees, small parcels of earth are very frequently enclosed in their interstices and behind them,— so perfectly that not a particle could be washed away during the longest transport: out of one small portion of earth thus *completely* enclosed by the roots of an oak about 50 years old, three dicotyledonous plants germinated: I am certain of the accuracy of this observation. Again, I can show that the carcasses of birds, when floating on the sea, sometimes escape being immediately devoured; and many kinds of seeds in the crops of floating birds long retain their vitality: peas and vetches, for instance, are killed by even a few days' immersion in sea-water; but some taken out of the crop of a pigeon, which had floated on artificial sea-water for 30 days, to my surprise nearly all germinated.

Living birds can hardly fail to be highly effective agents in the transportation of seeds. I could give many facts showing how frequently birds of many kinds are blown by gales to vast distances across the ocean. We may safely assume that under such circumstances their rate of flight would often be 35 miles an hour; and some authors have given a far higher estimate. I have never seen an instance of nutritious seeds passing through the intestines of a bird; but hard seeds of fruit pass uninjured through even the digestive organs of a turkey. In the course of two months, I picked up in my garden 12 kinds of seeds, out of the excrement of small birds, and these seemed perfect, and some of them, which were tried, germinated. But the following fact is more important: the crops of birds do not secrete gastric juice, and do not, as I know by trial, injure in the least the germination of seeds; now, after a bird has found and devoured a large supply of food, it is positively asserted that all the grains do not pass into the gizzard for twelve or even eighteen hours. A bird in this interval might easily be blown to the distance of 500 miles, and hawks are known to look out for tired birds, and the contents of their torn crops might thus readily get scattered. Some hawks and owls bolt their prey whole, and after an interval of from twelve to twenty hours, disgorge pellets, which, as I know from experiments made in the Zoological Gardens, include seeds capable of germination. Some seeds of the oat, wheat, millet, canary, hemp, clover, and beet germinated after having been from twelve to twenty-one hours in the stomachs of different birds of prey; and two seeds of beet grew after having been thus retained for two days and fourteen hours. Fresh-water fish, I find, eat seeds of many land and water plants; fish are frequently devoured by birds, and thus the seeds might be transported from place to place. I forced many kinds of seeds into the stomachs of dead fish, and then gave their bodies to fishing-eagles, storks, and pelicans; these birds, after an interval of many hours, either rejected the seeds in pellets or passed them in their excrement; and several of these seeds retained the power of germination. Certain seeds, however, were always killed by this process.

Locusts are sometimes blown to great distances from the land. I myself caught one 370 miles from the coast of Africa, and have heard of others caught at greater distances. The Rev. R.T. Lowe informed Sir C. Lyell that in November, 1844, swarms of locusts visited the island of Madeira. They were in countless numbers, as thick as the flakes of snow in the heaviest snowstorm, and extended upward as far as could be seen with a telescope. During two or three days they slowly careered round and round in an immense ellipse, at least five or six miles in diameter, and at night alighted on the taller trees, which were completely coated with them. They then disappeared over the sea, as suddenly as they had appeared, and have not since visited the island. Now, in parts of Natal it is believed by some farmers, though on insufficient evidence, that injurious seeds are introduced into their grass-land in the dung left by the great flights of locusts which often visit that country. In consequence of this belief Mr. Weale sent me in a letter a small packet of the dried pellets, out of which I extracted under the

microscope several seeds, and raised from them seven grass plants, belonging to two species, of two genera. Hence a swarm of locusts, such as that which visited Madeira, might readily be the means of introducing several kinds of plants into an island lying far from the mainland.

Although the beaks and feet of birds are generally clean, earth sometimes adheres to them: in one case I removed sixty-one grains, and in another case twenty-two grains of dry argillaceous earth from the foot of a partridge, and in the earth there was a pebble as large as the seed of a vetch. Here is a better case: the leg of a woodcock was sent to me by a friend, with a little cake of dry earth attached to the shank, weighing only nine grains; and this contained a seed of the toad-rush (Juncus bufonius) which germinated and flowered. Mr. Swaysland, of Brighton, who during the last forty years has paid close attention to our migratory birds, informs me that he has often shot wagtails (Motacillæ), wheatears, and whinchats (Saxicolæ), on their first arrival on our shores, before they had alighted; and he has several times noticed little cakes of earth attached to their feet. Many facts could be given showing how generally soil is charged with seeds. For instance, Professor Newton sent me the leg of a red-legged partridge (Caccabis rufa) which had been wounded and could not fly, with a ball of hard earth adhering to it, and weighing six and a half ounces. The earth had been kept for three years, but when broken, watered and placed under a bell glass, no less than 82 plants sprung from it: these consisted of 12 monocotyledons, including the common oat, and at least one kind of grass, and of 70 dicotyledons, which consisted, judging from the young leaves, of at least three distinct species. With such facts before us, can we doubt that the many birds which are annually blown by gales across great spaces of ocean, and which annually migrate — for instance, the millions of quails across the Mediterranean — must occasionally transport a few seeds embedded in dirt adhering to their feet or beaks? But I shall have to recur to this subject.

As icebergs are known to be sometimes loaded with earth and stones, and have even carried brushwood, bones, and the nest of a land-bird, it can hardly be doubted that they must occasionally, as suggested by Lyell, have transported seeds from one part to another of the arctic and antarctic regions; and during the Glacial period from one part of the now temperate regions to another. In the Azores, from the large number of plants common to Europe, in comparison with the species on the other islands of the Atlantic, which stand nearer to the mainland, and (as remarked by Mr. H.C. Watson) from their somewhat northern character, in comparison with the latitude, I suspected that these islands had been partly stocked by ice-borne seeds during the Glacial epoch. At my request Sir C. Lyell wrote to M. Hartung to inquire whether he had observed erratic boulders on these islands, and he answered that he had found large fragments of granite and other rocks, which do not occur in the archipelago. Hence we may safely infer that icebergs formerly landed their rocky burdens on the shores of these mid-ocean islands, and it is at least possible that they may have brought thither the seeds of northern plants.

Considering that these several means of transport, and that other means, which without doubt remain to be discovered, have been in action year after year for tens of thousands of years, it would, I think, be a marvellous fact if many plants had not thus become widely transported. These means of transport are sometimes called accidental, but this is not strictly correct: the currents of the sea are not accidental, nor is the direction of prevalent gales of wind. It should be observed that scarcely any means of transport would carry seeds for very great distances; for seeds do not retain their vitality when exposed for a great length of time to the action of sea water; nor could they be long carried in the crops or intestines of birds. These means, however, would suffice for occasional transport across tracts of sea some hundred miles in breadth, or from island to island, or from a continent to a neighbouring island, but not from one distant continent to another. The floras of distant continents would not by such means become mingled; but would remain as distinct as they now are. The currents, from their course, would

never bring seeds from North America to Britain, though they might and do bring seeds from the West Indies to our western shores, where, if not killed by their very long immersion in salt water, they could not endure our climate. Almost every year, one or two land-birds are blown across the whole Atlantic Ocean, from North America to the western shores of Ireland and England; but seeds could be transported by these rare wanderers only by one means, namely, by dirt adhering to their feet or beaks, which is in itself a rare accident. Even in this case, how small would be the chance of a seed falling on favourable soil, and coming to maturity! But it would be a great error to argue that because a well-stocked island, like Great Britain, has not, as far as is known (and it would be very difficult to prove this), received within the last few centuries, through occasional means of transport, immigrants from Europe or any other continent, that a poorly-stocked island, though standing more remote from the mainland, would not receive colonists by similar means. Out of a hundred kinds of seeds or animals transported to an island, even if far less well-stocked than Britain, perhaps not more than one would be so well fitted to its new home, as to become naturalised. But this is no valid argument against what would be effected by occasional means of transport, during the long lapse of geological time, whilst the island was being upheaved, and before it had become fully stocked with inhabitants. On almost bare land, with few or no destructive insects or birds living there, nearly every seed which chanced to arrive, if fitted for the climate, would germinate and survive.

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