

The Flora and Fauna of the Isle of Man and their Geographical Relationships

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For too long the Isle of Man has been omitted from discussions concerning the history of the flora and fauna of the British Isles. This has been due not so much to a deliberate disregard of the interesting problems posed by the island, but more to the fact that the relevant material is hidden in obscure places scattered through various journals. It seemed to the authors that this state of affairs, however much it was deplored, would continue until someone familiar with the literature made an attempt at a synthesis, incomplete though it might be, in order to bring much of this scattered data together in one place. There also seemed every likelihood of the work and conclusions of botanists remaining unknown to zoologists, and *vice versa*, unless a summary of all that has been discovered so far was presented in a single paper.

The compiling of a summary of this sort, especially when none has been attempted previously, is a difficult undertaking. We have been forced to concentrate on those particular groups with which one of us happens to be familiar, making but passing reference to the cryptogams and certain zoological orders, which in any case have been too little studied to produce many valid generalisations. Attempts at comparisons with neighbouring areas are again beset with difficulties, for the requisite information is very scattered and tends to change rapidly with the passing of time. In the groups that receive the widest attention we are confident that our data are reasonably up-to-date and accurate, but it has proved next to impossible to check thoroughly the validity of the comparisons made in the more abstruse groups. In this matter we must ask for forbearance and trust that inaccurate assumptions on distributional questions will come to the notice of the specialists concerned, subsequently to be corrected, and that the shortcomings of this paper will be outweighed by its usefulness.

The island is only thirty-three miles long and twelve at its widest point, and consequently it is nearly one hundred and forty-three times smaller than Ireland. It is important to remember this relatively small surface area when making comparisons with Ireland and Great Britain. Many species that might be expected to occur are absent not merely as a result of early insulation but because the island fails to provide in the available area the ecological conditions necessary for their existence. Thus the rivers are too small to hold Otters, *Lutra lutra* (L.), and the streams too few to afford a rich freshwater fauna and flora — only six species of freshwater fish are known to be indigenous — the hill-tops are bare of exposed rock, so that the flora is markedly lacking in rupestral species, and there is also virtually no calcareous soil.

The most striking feature, however, and the one - which has perhaps had most effect on the present composition of the flora and fauna, is the remarkable paucity of woodland. Except in the larger glens, the island is all but bereft of any considerable aggregation of native trees. In the seventeenth century the island seems to have been even barer than to-day in the absence of the plantations that have since grown up. As early as 1098 there was apparently not enough large timber left for building forts and Magnus Barefoot, King of Norway, had to import the amount he required from Galloway. The evidence for inferring the ancient extent of forest is somewhat ambiguous. On the one hand, we should expect a dense forest cover in the lowlands on ecological grounds, and this is supported by the recent archaeological discovery that in time first centuries A.D. the

people lived in large earth-covered round-houses, the construction of each of which involved the use of several thousand oak posts. The *Chronicon Manniae* records that great woods still existed, especially in the north, as late as the eleventh century; but in 1521 an English legal document mentions that according to Manx customary law the stealing of an ox or a horse is considered no felony because the absence of woods renders any attempt to conceal these animals out of the question. On the other hand, we must set against this evidence the fact that in samples of peat from the Strandhall submerged "forest" (Bruce 1928, Erdtman 1928) tree pollen was found to be remarkably scanty. This peat has been ascribed to the Sub-boreal Period, but there is nothing in the data to prove that it could not be much more recent.

These few clues that have come down to us seem to suggest that time period of maximum forest clearance coincided with the Norse occupation. At present many characteristic woodland plants, such as *Mercurialis perennis* L., *Poa nemoralis* L. and *Bromus ramosus* Huds., appear to be completely missing, and the same applies to many of the larger fungi, corticolous lichens and wood-feeding beetles. Other absentees, normally characteristic of woodland, include the Badger, *Meles meles* (L.), Jay, *Garrulus glandarius* (L.) and Bullfinch, *Pyrrhula pyrrhula* (L.). It is reasonable to assume that a considerable number of woodland species, which formerly occurred, must have become extinct when their habitat was so largely destroyed. There are, in fact, scraps of folk-lore that suggest that the Fox, *Vulpes vulpes* (L.) may once have been an inhabitant of the island.

The climate, in addition, has played an extremely important part in influencing distribution. It is a byword in the Isle of Man that the weather is completely unpredictable and understood by no one. Briefly, the island enjoys a characteristically oceanic type of climate, with cool summers, mild winters, very slight frosts and a rather high rainfall. The last mentioned, however, displays great variation in different parts of the island, ranging from over sixty inches in the mountains to twenty-five on the south coast; also, in view of the uniformity of the surface geology (apart from the northern alluvial plain) the island presents exceptional opportunities for the study of distribution patterns produced by local climatic differences. The cool summer makes harvests late and prevents fruit from ripening, while it also has a very notable effect on flowering periods, many spring flowers appearing again in autumn or even almost throughout the year. The mean winter temperature is higher than that of any county in the south of England with the exception of Cornwall, and for an Atlantic climate the amount of sunshine is unusually high. Not unexpectedly, the vegetation is lush, many exotics flourish, and the fauna and flora both display a predominantly western aspect.

The oceanic climate often causes an interesting geographical differentiation between allied forms of plants and animals. Thus, the more westerly representative tends to occur in all parts of the island, while the other is confined to the eastern and southern periphery. Such var. is the case with the grass *Arrhenatherum elatius* (L.) J. & C. Presl *elatius*, which is all but replaced by var. *bulbosum* (Wind.) Spenn. and similarly with the fern *Polypodium vulgare* L., in which the hexaploid form almost completely supplants the tetraploid.

Species of a markedly western type of distribution present in the island include *Wahlenbergia hederacea* (L.) Rchb., *Pinguicula lusitanica* L. and *Carex punctata* Gaud. among the flowering plants and *Adiantum capillus-veneris* L. among the ferns; the insects include the moth *Aegeri philanthiformis* (Lasp.), the beetles *Barypithes sulcifrons* (Boh.) and *Tachyporus obtusus* (L.) var. *nitidicollis* Steph., and the dragonfly *Sympetrum striolatum* (Charp.) ssp. *nigrifemur* (Selys). Many of the most extreme western species are, paradoxically, confined (or virtually so) to the central part of the east coast, which has a considerably higher rainfall than the west. These include the Welsh Poppy, *Meconopsis*

cambrica (L.) Vig. and *Carex punctata* Gaud. among the flowering plants and *Pottia crinita* Wils. var. *viridifolia* (Mitt.) Moenk. among the mosses, as well as the Manx Lepidopterous specialities *Antitype mista* (Huebner), *Hadena caesia* (Schiff.) var. *lepida* (Esper) var. *capsophila* Duponchel.

The absence of species with a Hiberno-Pyrenean range, with the single exception of *Hadena cassia* (Schiff.), is in marked contrast to Ireland. It is, however, now coming to be generally accepted that the much-discussed "Lusitanian" element in the British Isles is merely the extreme of a series linking up species with an otherwise wholly Mediterranean range with others of a general south-westerly, sub-Atlantic type of distribution; and so the explanation of the origin of this element is much simpler than has been made out. In the same way it is impossible to draw any sharp dividing line between the western and the southern species in the Isle of Man. One group might, in fact, be termed south-western: it comprises a number of species occurring in south (especially south-west) England, west Wales and Cumberland or Galloway, but not in Ireland. Its representation in Man include the Isle of Man Cabbage, *Rhynchosinapis monensis* Dandy, the grass, *Bromus ferronii* Mabille, the moss, *Leptodon smithii* (Hedw.) Mohr, the moth *Antitype xanthomista* (Huebner), the beetle *Meligethes exilis* Sturm. and the plant-bugs (Hemiptera) *Corizus hyosciami* (L.) and *Gampsocoris punctipes* (Germ.). The Jasione moth, *Eupithecia denotata* (Huebner) ssp. *jasioneata* Crewe, extends this type of distribution by occurring in the south-west of Ireland as well. A number of other species characteristic of south England occur in Man, but in Ireland are confined to the south-east corner; they include the flowering plants *Ranunculus parviflorus* L. *Trifolium scabrum* L. and *Orobanche rapum-genistae* Thuill. the moss *Philonotis rigida* Brid., the moth *Eilema caniola* (Huebner), the water-beetles *Bidessus minutissimus* Germ. and *Cymbiodyta ovalis* Thoms. and the Speckled Bush-cricket *Leptophyes punctatissima* (Bosc.).

A very interesting group of species with a "Continental" or Central European type of range, mostly absent or very rare in Ireland, is concentrated in the north-west corner of the island, principally on sandy heathland. These species appear to be relics of a xerothermic period in early post-glacial times and may have found survival here easier than elsewhere in the British Isles owing to the more feeble spread of the forest cover. They include the flowering plants *Astragalus danicus* Pets., widespread round the south and west coasts but only in the Aran Isles in Ireland, *Genista tinctoria* L., *Hypochaeris glabra* L., a very hairy form of *Euphrasia curta* (Fries) Wettst., *Rumex tenuifolius* (Wallr.) Lore, *Koeleria albescens* DC. and possibly also *Helianthemum guttatum* (L.) Mill., for which there is a very old unlocalised record for Man that cannot be dismissed as an error; also the Sand Lizard, *Lacerta agilis* L. the water-beetle *Ilybius subaeneus* Erickson and the spider *Lyrosa prativaga* L.K. The rare *Ichneumon primatorius* Forster, for some curious reason confined to the Calf islet, apparently belongs to this group too. The Pug moth *Eupithecia alliaria* Staud. was recently taken near Ballaugh in this same north-west corner; previously it had only been known from south France, Austria, Hungary and Asia Minor, and since its food plant, *Allium flavum* L. is not British, it may have been only an accidental vagrant. Even so, there are plants of the "Continental" type, such as *Inula salicina* L. and *Orchis cruenta* O. F. Muell., which occur in Ireland but miss Great Britain, and it is not impossible that the Isle of Man, may harbour relic populations of species that have become extinct in other parts of the British Isles.

To complete the geographical mosaic there is also a substantial northern element. The mountain fauna and flora are, however, very meagre when compared with, for example, the Isle of Arran. The mountains are all under 2,050 feet and for the most part consist of bare moorland. The very few arctic-alpine species that survive on some of the summits are all extremely local they include the willow, *Salix herbacea* L. (common in the Manx Late-glacial deposits), the moss, *Plagiothecium Muehlenbeckii* B. & S., one or

two lichens and the beetles *Otiorrhynchus dubius* (Stroem) and *Arpedium brachypterum* (Gray.). In addition there are certain mountain species which favour lower levels. The northern beetle *Otiorrhynchus arcticus* (Fabr.) var. *biandus* Gyll. mostly occurs between 300 and 500 feet and even descends to sea level. The prevalence of flowering plants such as *Orchis purpurella*. T. & T. A. Steph., *Lamium molucellifolium* Fries and *Cochlearia scotica* Bruce also lends a northern aspect to the lowland vegetation. Other northern species recorded include the moss, *Homomallium incurvatuni* (Brill.) Loeske, the Scotch Argus butterfly *Erebia aethiops* (Esp.), the moth *Hadena glauca* (Huebner.), several beetles including *Barynotus squamosus* Germ. var. *Schonerri* (Zett.), *Melolontha hippocastani* Fehr., *Hydraena gracilis* Germ., *Nebria gyllhenhali* (Sch.), *Hydroporus morio* Aube and *H. tristis* Payk., the water-bug *Corixa germari* Fieb. and the stonefly *Diura bicaudata* (L.). The lichen flora is reported (Hartley & Wheldon 1927) to be remarkably poor in boreal types, and the same is true of the water-beetles (Balfour-Browne 1911). Perhaps more western than northern is the golden yellow var. *aureus* Wilm. of the Wild Radish, *Raphanus raphanistrum* L. and the very dark form *scotica* Watkins of the Dark Green Fritillary *Arginnis aglaja* (L.), both of which occur in the Hebrides, Man and Cornwall or the Scillies.

There are a few animals (but apparently no plants) which are confined to Ireland and the Isle of Man and not found in Great Britain. These include the Irish Stoat—*Mustela erminea hibernicus* (Thomas & Barr.-Ham.), the moths *Hadena caesia* (Schiff.) var. *manani* Gregson and *H. lepida* (Esper) var. *capsophila* Duponchel, the beetle *Phosphuga subrotundata* Leach (which is widespread in the island) and the earth worm *Lumbricillus evansii* Southern. The most variable of those species of Lepidoptera common to both Britain and Ireland tend rather toward the Irish forms in Man. Thus the Meadow Brown *Maniola jurtina* (L.) includes noticeably bright individuals very like the Irish form *inernes* Graves, which in its turn (Beirne 1952) resembles the southern European form *hispulla* rather than the form common in Great Britain. Many specimens of the Wall Butterfly *Dira mergera* (L.) are also large than the British type and more like the Irish one. The Coal-Titmouse *Parus ater* L. presents a rather similar analogy; R. Wagstaffe (private communication) finds that most examples appear to be identical with *britannicus* Sharpe & Dress., but cheeks of adults in fresh plumage. very occasionally exhibit a faint yellowish tinge, thus approaching the Irish *hibernicus* O. Grant. The Manx Hare is said (Kermode 1889, Moffat 1928) to possess characteristics of both the Irish race *Lepus hibernicus* Bell and the English one *L. occideatulis* de Winton, but further investigation is needed on this point, the Hare, despite statements to the contrary, does appear to be native, for its remains have been found associated with a Mesolithic culture at Port St. Mary. Similar uncertainty surrounds the Dipper (a very rare bird in Man): of three specimens which he compared with skins in museums the P. G. Ralfe thought two resembled the British race *Cinclus cingularis* (Latham) while the third was more similar to *C. cinclus hibernicus* O. Grant. The Manx Hare is said (Kermode 1889, Moffat 1928) to possess characteristics of both the Irish race, *Lepus hibernicus* Bell and the English one *L. occidentalis* de Winton, but further investigation is needed on this point – the hare despite statements to the contrary, does appear to be native, for its remains have been found associated with a Mesolithic culture at Port St. Mary. Similar uncertainty surrounds the Dipper (a very rare bird in Man) of three specimens he compared with skins in museums the late P. G. Ralfe thought two resembled the British race *Cinclus cinclus gularius* (Latham) while the third was similar to *C. cinclus hibernicus* Hart., the race of Ireland and west Scotland, but H. F. Witherby hesitated to refer it definitely to either. R. Wagstaffe has recently reexamined one of these specimens but finds it impossible to place satisfactorily owing to fading. As in Ireland, the Hooded Crow, *Corvus cornix* L. largely replaces the Carrion Crow, *C. corone* L. and the two interbreed—apparently less rarely than in Ireland.

The mingling of different geographical races and the presence of individuals with intermediate characters is perhaps the most striking feature of the Manx fauna and flora. In early post-glacial times we must envisage the Irish Sea bed as having been a low undulating plain. Belts of species with varying degrees of preference for oceanic or other conditions would have stretched across this plain, often with distinct western and eastern races overlapping in range and maybe forming a hybrid zone, which in its turn might come to present the appearance of a cline. These belts must have fluctuated in response to the post-glacial climatic and ecological changes: homozygotes of the western races may have been stranded, at the close of periods of expansion, far to the east of their main populations and vice versa. It is clear that many of the apparently endemic forms in Ireland are really relics surviving in a peripheral region, and their former presence in Great Britain is indicated by the occurrence of intermediates in the western parts of the latter island. Thus, intermediates between the British form and the Irish and Manx form of the moth *Hadena lepida* (Esper) occur in South Wales and other westerly areas; and, again, intermediates between British and Irish Coal-Titmice—*Parus ater* L. occur both in South Wales and north-east Ireland. It has also been suggested (Beirne 1952) that the Stoat of Jura and Islay, *Mustela erminea ricinae* Mill., may be the product of ancient crossing between the British Stoat *M. erminea stabilis* Barr.-Ham. and the endemic Irish and Manx *M. erminea hibernicus* (Thomas & Barr.-Ham.).

It is essential to bear these facts in mind when considering the phenomena of hybridization in the Isle of Man. The island seems to have acted as a refuge for closely related species and races and their hybrids to an extent with which few other areas in the British Isles can compare. On top of this, the somewhat artificial conditions involved in a wholly insular existence have led to certain interesting anomalies. For example, it is not uncommon for heterozygotes of an intermediate appearance to be much more plentiful in the island than either of the pure homozygotic extremes, and even for one of the latter to be entirely lacking. The dragonfly *Sympetrum striolatum* (Chap.) is predominantly represented by the form *nigrifemur* (Selys), but while intermediates tending towards typical *striolatum* are frequently met with, as in Ireland and Wales, the typical form has only been encountered on a single occasion. A similar situation is presented by the Water Purslane--*Peplis portula* L., which exhibits a cline in the length of the calyx teeth: the eastern type and intermediates are about equally frequent, while the western extreme is curiously rare. The critical group of Water Blinks—*Montia fontana* L. provides a parallel instance in that ssp. *variabilis* Walt., a rather variable but more or less fixed hybrid between the northern ssp. *fontana* and the western asp. *inter-media* (Beeby) Walt., is common over most of the island, while of the parents the former is apparently absent and the latter known only from a single locality. Rather similar again are those cases involving certain species pairs among flowering plants, in which one of the parents is very rare or absent, while the hybrid, though quite sterile, is relatively widespread. The Watercress—*Rorippa nasturtium-aquaticum* (L.) Hayek is frequent, in the south and east in regions near the sea, but, although *R. microphylla* (Beenn.) Hyl. appears to be extinct, their hybrid has been found in many localities all over the southern half of the island. Similarly, the sterile hybrid between the two grasses *Glyceria fluitans* (L.) R. Br. and *G. plicata* (L.) R. Br. is considerably more widespread than the latter parent; and an identical situation applies in the case of the sterile hybrid between the two Water Speedwells--*Veronica anagallis-aquatica* L. and *catenata* Pennell.

The great extent of hybridization proceeding in the Isle of Man, as in Ireland, is the outcome not only of climatic oscillations and their influence in causing the ranges of species that are normally well separated to overlap, but also of human interference in its manifold aspects, such as forest clearance, cultivation, grazing by domestic

animals and the introduction of rabbits. Among flowering plants hybridization, even to the point of introgression, is prevalent in the genera *Metandrium*, *Potentilla*, *Rosa*, *Euphrasia* and *Senecio* in particular. At the same time, many plants and animals exhibit anomalous ecological behaviour, as a result of the reduced pressure of competition in a flora and fauna impoverished by early and prolonged isolation, together with the effects of the prevailing oceanic climate. Thus the water-beetle *Hydraena testacea* Curt. occurs among stones in the Sulby river, although it is normally an inhabitant of stagnant ditches and ponds (Balfour-Browne 1911); and, similarly, the presence in lowland streams of the stonefly *Diura bicaudata* (L.) (Hynes 1952) is interesting, for in Great Britain and apparently also in Ireland it is confined to streams at high levels and to lakes. The flowering plants afford further instances: because of the lack of salt-marshes, *Scirpus maritimus* L., *Juncus maritimus* L. and *Schoenus nigricans* L. grow in rock-pools on the coast, while many species normally common inland, such as *Coronopus squamatus* (Forsk.) Aschers. *Sedum. acre* L., *Eupatorium. cannabinum* L. and *Thymus Drucei* Ronn. em. *Jalas*, become almost exclusively confined to the immediate vicinity of the sea.

Because of their isolation insular populations are well-known to be prone to some degree of differentiation. Time increased amount of in-breeding necessitated provides greater opportunities for the combination of recessive genes in a homozygous condition. Great fluctuations in numbers, such as occur among insects, may result in an excessive reduction of the population to such a low level that many recessives may become eliminated without any chance of replacement, causing the variation in consequence to follow a different trend. An example of the operation of these factors is presented by the unusually high percentage in Man of the rare variant of the Orange Tip butterfly—*Euchloë cardamines* (L.) in which the orange tips on the forewings are replaced by pale yellow. When this species, after a long period of great rarity, suddenly began to spread after 1937 in many parts of the island, no less than five specimens of this variant were taken in a single year. Curiously enough, the Manx examples of the Orange Tip are all very bright and probably represent a distinct subspecies. The sudden increase of an endemic race has a parallel in the phenomenal spread of the Irish Jay—*Garrulus glandarius hibernicus* With. & Hart. all over Ireland since the last century. Some notable variants of the Harebell—*Campanula rotundifolia* L. have also been encountered in the north-west corner. and a form of the Maidenhair Fern—*Adiantum capillus-veneris* L. var. *rotundum* Newm. with narrower fronds, rounded pinnulas and hardier development was collected in the island in 1841 and has long been in cultivation. Such cases suggest incipient endemism.

There is a striking lack of endemics among the plants compared with their frequency among the animals, although this lack may be apparent rather than real owing to inadequate study. A new Asilid or robber-fly, *Epitriptus cowini* Hobby, discovered inhabiting very limited areas in two quite different parts of the island between 1939 and 1949, was found in one of its stations feeding on a small pug moth *Eupithecia alliaria*. Staud., which in its turn was new to the British Isles. Recent work by Wagstaffe (private communication) on the birds of the island has detected endemic tendencies among a few species : the Robin—*Erithacus rubecula* (L.) is on the average slightly darker than the British bird, a characteristic which is particularly marked in specimens from the Currags; the Hedge-Sparrow—*Prunella modularis* (L.) is slightly darker, and the Goldfinch - *Carduelis carduelis* (L.) on the average slightly smaller than the British bird; specimens of the Magpie—*Pica pica* (L.) examined were on the whole generally smaller and with relatively deeper bills, but they can be matched by examples on the mainland; finally, specimens of the Stone-Chat—*Saxicola torquata*, (L.) were found to be slightly darker than *hibernans* (Hart.), but some British specimens are identical and none are as dark as the West Scottish race *theresae* Meinertzhagen.

Peculiar local variations in the Lepidoptera have been repeatedly noted, and there is space here to mention only a very few: the lists given in the literature (Clarke 1892, Hedges 1947) should be consulted for fuller details. It was at one time asserted (Birchen 1880) that the Manx form of the Small Tortoiseshell—*Aglais urticae* (L.) is always remarkably small, a specimen rarely being found to equal the smallest English specimens; but H. S. Clarke some years later declared that he could detect no such constant difference. *Atethmia centrago* (Haw.) is widespread, but a special form with darker and more uniform colouring, var. *unicolor* Stand., is confined to the Pulrose district and is interesting in most closely resembling the form of the species found in Central France. The Manx specimens of the Dew Moth—*Setina irrorella* Clerck appear to be darker and more richly marked than English ones, while *Phragmatobia fuliginosa* (L.) is also very dark and the island is said to be richer in varieties than any other known locality by Clarke, who remarked that he had never seen the typical form in Man. Extremely dark forms of the Garden Dart—*Euxoa nigricans* (L.) also occur and the Manx forms of *Hadena caesia* (Schiff.) and *H. lepida*. (Esper) are both darker than the Irish ones. But despite these numerous local variations there appears to be no actual species among the Lepidoptera that can be claimed as endemic.

In the past several authors have denied the possibility of a post-glacial land connection with Great Britain. This view has been maintained in spite of the shallow seas (nowhere more than 130 feet in depth) that intervene between the Isle of Man and the eastern coast of the Irish Sea. At one time it was thought (Kendall 1894) that the indigenous flora and fauna were so extraordinarily poor in species that this phenomenon could only be accounted for by supposing random transmarine migration. That birds, winds and sea currents have each played a part in stocking the island cannot be denied, but these factors have so often been invoked in the past merely for want of a better explanation that it is not unreasonable for present-day students of plant and animal dispersal to maintain an attitude of healthy scepticism about them. Demonstrative proof is only too often lacking, and modern advances in ecological knowledge suggest that transmarine dispersal usually requires an abnormally high degree of coincidence if transported organisms are to chance upon exactly the right ecological requirements, without which they would undoubtedly perish within a very short time. In any case, it is unnecessary to drag these factors into the present discussion in view of the apparently quite satisfactory geological explanation to be considered presently; all that can be said is that such factors have doubtless played a part, but probably a very minor one.

It is now clear that if the lack of certain types of habitat is taken into full consideration, the flora and fauna are really surprisingly rich. The old view cited above was therefore based on false premises. Moreover, we must take into account the continuing diminution characteristic of insular populations, for which a slight fluctuation below the minimum survival density can be fatal as well as irreparable. Such, indeed, may have been the case with several species which seem to have become extinct from natural causes, such as the Greater Burnet *Sanguisorba officinalis* L. which occurred in Late-glacial times and for which acres of suitable ground still exist in the Currags. The total absence of any voles has also been used as an argument against a land connection. Either the island ---and Ireland too---was isolated before voles could spread to it, which, though perfectly possible, seems hard to believe, or they were kept out by adverse ecological conditions, or else some did arrive but have been wiped out. This third alternative is a purely negative one, for no remains have been found in the early post-glacial deposits.

Other authors (Carpenter 1897, Bailey 1908) have postulated a land-bridge connecting Man directly with Ireland as well as with Britain. Since a long and very deep trough separates the two former islands, it is necessary to place this hypothetical bridge either between Anglesey and Dublin or to the north between

Antrim and Scotland. It has since, however, been pointed out (Balfour-Browne 1911, Deevey 1949) that the presence of Irish forms in Man can be explained quite satisfactorily without invoking any such land-bridge between the two; the only requisite is a land connection between Man and Britain.

The authority on the island's geology (Lamplugh 1903) also rejected the possibility of any post-glacial land connections, making the ingenious, but unconvincing, suggestion that the Irish Elk—*Cervus giganteus* (Blumenbach) contrived to enter the Isle of Man at the close of the Ice Age and leave its remains there by crossing over the sea when it was frozen. Previously, it had been the very presence of this large and cumbrous creature in the island that had been the main plank in the argument of the supporters of a land-bridge (Dawkins 1898). A recent discussion of certain peculiar absentees among the Plecoptera (Hynes 1952) has lent some support to Lamplugh's views.

The evidence in favour of a land connection persisting for some time after the close of the Ice Age now seems overwhelming. The geographical patterns of the fauna and flora are too convincing to be explained away as the results of mere random dispersal. And what of the presence of completely flightless insects like the Orthopteroid *Leptophyes punctatissima* (Bosc.)? The Irish Elk and the Red Deer *Cervus elaphus* L.—the latter is now definitely known to have been once indigenous in the island (Allen 1952) - could hardly have entered otherwise than over dry land, if we dismiss the far-fetched ice-bridge theory. Certain alien influences from the Continent that affected the Mesolithic culture in the Isle of Man but did not penetrate to Ireland are also believed (Clark 1932) to have arrived across dry land from Britain. There is general agreement that during the Ice Age all organisms in the region now represented by the Isle of Man, except perhaps for a handful of arctic types, must have been extinguished or banished far to the south by the ice sheets and the rigours of the accompanying climate. Restocking must have begun very soon after the melting of the ice and continued with increasing momentum till the assumed severance occurred in early post-glacial times.

There is every reason to believe that the sea-level during the Ice Age fell at least 400 feet, which would leave the bed of the Irish Sea entirely dry except for a narrow lake off Ireland (Godwin 1949). By the end of the Pre-Boreal period, c. 7500 B.C., the climate had become relatively warm and large stretches of open countryside still survived before the forest cover had managed to spread and block any further migration of plants and animals at the rapid rate possible up till then. The increasing warmth during the ensuing Boreal period produced a rapid melting of the ice, resulting in a eustatic rise in sea-level of considerable speed and magnitude. It is probable that the final severance of Ireland took place in the vicinity of the shallows between Scotland and the north Irish coast early in the Boreal period (Mitchell 1952). The insulation of the Isle of Man must have taken place some time later, probably through the convergence of two arms of the sea passing to the north and south of the island respectively. The early part of the Boreal period has been suggested (Bruce 1928) as a probable date for this occurrence. However, taking into account the much shallower seas separating Man from Britain and the various species found in the island that are missing from Ireland, a date more towards the middle of the Boreal period, say 6800 B.C., might be nearer the truth. Pollen analysis work in the future may be expected to establish the date of the severance with greater precision than is at present possible. It should perhaps be added that various other authorities (e.g. Charlesworth 1936, Gresswell 1938, Movius 1940) have accepted a fall in sea-level of about 120 feet, which is attested by clear geomorphological evidence in the Irish Sea area; such a fall would result in the coastline coinciding with the present 22-fathom depth contour, so that even on this conservative estimate the Isle of Man would have been joined to

Britain prior to the post-glacial advance of the sea. It has also been suggested (Gresswell 1947) that with the recession of the sea at the termination of the 25-foot Raised Beach, c. 2500 B.C., the land connection with the Isle of Man might have been temporarily re-established. This seems unlikely, but it is a possibility that ought not to be overlooked.

A strong argument against extensive transmarine dispersal is the remarkable absence of many species found all round the Irish Sea and even abundant in some counties. Thus the paucity of Hawkweeds (*Hieraceum* spp.), despite their wind-blown fruits, is a very interesting feature of the Manx flora, for suitable habitats occur in plenty. Similarly, several winged species of Plecoptera that are common in Britain in habitats equally available in Man (Hynes 1952) are curiously absent. Several species of flowering plants are also missing although known from every county bordering on the Irish Sea, and their absence cannot be attributed to the lack of suitable habitats or edaphic factors. They include *Thalictrum flavum* L., *Ranunculus trichophyllus* Chaix, *Hypericum dubium* Leers, *Geum rivale* L. *Apium graveolens* L., *Oxycoccus palustris* Pers., *Juncus inflexus* L. and *Rhynchospora alba* (L.) Vahl. Surprising absentees among insects include the water-beetle *Orcodytes rivalis* (Gyll.), several species of Plecoptera including *Porlodes mortoni*; (Klapalek), and the Large Heath butterfly *Coenonympha tullia* (Muell.).

In general, species that are absent from Ireland are also absent from the Isle of Man. Both islands are devoid of snakes and voles, of the Common Shrew—*Sorex araneus* L., the Tawny Owl—*Strix aluco* L., all Woodpeckers (*Picus viridis* L. and *Dryobates* spp.), the Nuthatch—*Sitta europaea* L., the Hawfinch—*Coccothraustes coccothraustes* (L.), the Willow-Titmouse—*Parus atricapillus* L. and Marsh-Titmouse—*P. palustris* L., and also it would appear the Meadow Grasshopper—*Chorthippus parallelus* (Zett.). Man also agrees with Ireland (and not with England in the absence or rarity of various small summer migrants among the birds.

But there is also a sizeable group of species that the island shares with Great Britain and not with Ireland, evidently to be interpreted as the consequences of its later severance. Non-Irish flowering plants comprise *Rhynchosinapsis monensis* (L.) Danby, *Dianthus armeria* L. (probably native), *Stellaria nemorum* L., *Genista tinctoria* L., *Vicia lutea* L., *Valeriana dioica* L., *Hieracium vagum* Jord., *H. bladonii* Pugsl. (the Irish specimens so named all belong to a distinct endemic species, according to Mr. P. D. Sell and Dr. C. West), *Rumex tenuifolius* (Wallr.) Löve, *Salix cinerea* L., *Koeleria, albescens* DC., and *Bromus Ferronii* Mabilie. The mosses support this evidence with *Sphagnum Warnstorffianum* Du Metz, *Leptodon. Smithii* (Hedw.) Mohr, *Plagiothecium Muehlenbecckii* B. & S. and *Homornallium incurvatum* (Brid.) Loeske. The Sand Lizard—*Lacerta agilis* L., recorded by Edward Forbes and perhaps lately rediscovered, is also absent from Ireland, as is the Warty Newt—*Triturus cristatus* (Laurenti), an old record of Forbes's which lacks verification. To these may be added the Scotch Argus—*Erebia aethiops* (Esp.), the moth *Antitype xanthomista* (Huebie) a number of beetles including *Ilybius subacneus* Erichson, *Potosia floricola* (Herbst), *Medon. ripicola* (Krantz), *Apion confluens* Kirby and *A. punctigerum* (Payk.), the possibly introduced amphipod *Gammarus pulex* (L.) and the woodlice (Isopoda) *Trichoniscoides sarsi* Patience, *Porcellio ratzeburgii* Brandt, *Metopornorthus pruinosis* Brandt (not native in Ireland) and *Armadillium picturn* Brandt, Most of these species are southern or eastern in range, but one or two are distinctly northern and occur in Scotland. Furthermore, certain species that are exceedingly scarce in Ireland contrive to occur in Man; these include the Pearl-bordered Fritillary—*Argynnis euphrosyne* (L.) and the Dew Moth—*Setina. irrorella* Clerck, which in Ireland are confined to the Burren, the mosses *Fissidens crassipes* Wils. and *Hypnum imponens* Hedw., and the water-beetle *Agabus labiatus* (Brehm).

Some broad assessment of the geographical flora and fauna must be attempted by way- of conclusion. From a floristic point of view the nearest resemblances are to Wigtownshire and north-east Ireland. Certainly the flora has very little in common with that of west England, which is said (Balfour-Browne 1911) to be the region to which the aquatic Coleoptera bear the closest kinship. Enough has *been* said already to show that the Isle of Man is a biogeographical 'half-way house' between Britain and Ireland, with a slight bias in favour of the latter. It cannot be too strongly emphasised, however, that our knowledge of many groups is still very imperfect, indeed wholly deficient in some cases. While such a state of affairs persists, it would be premature to make too many generalisations.

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