

The Testimony of the Endemic Species of the Canary Islands in Favour of the Age and Area Theory of Dr. Willis.

BY

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MANY botanists of eminence have interested themselves in the Canarian flora, and much has been written about it. An abundance of materials is, therefore, at our disposal, enabling us to appreciate the methods followed in dealing with the endemic species and the standpoints adopted with regard to the problem of their origin. It is to these two subjects that the following remarks will be entirely devoted.

Like most archipelagos that with other adjacent groups of islands go to form a separate floral region, the Canary Islands display a double endemism, the endemism peculiar to the group and the endemism that it shares as a member of the floral region. There are the endemic species peculiar to the archipelago, the Canarian proper, and there are the endemic species which it holds in common with the other groups of the Macaronesian floral region, the Azores, the Madeiras, and the Cape Verde Islands. The true Canarian endemic species number about 400, whilst the Macaronesian species, which occur in other Macaronesian groups but are not known from any other floral region, number about fifty. As far as my researches indicate, this disproportion is typical of insular floral regions.

The Macaronesian endemics are far more generally distributed over the Canary Islands than are the Canarian proper. From the materials supplied by Christ and by Pitard and Proust it appears that whilst only 8 per cent. or 10 per cent. of the Macaronesian endemic species have been recorded from one island only, between 60 per cent. and 65 per cent. of the Canarian endemics are only known from single islands. On the average the Macaronesian endemics occur in three or four islands (3.5), but the Canarian are found in only one or two (1.7).

The following tables have been prepared by the writer from the work of Pitard and Proust:

A.

Distribution in the Canary Islands of *Macaronesian* endemic species—that is, of species restricted to that floral region, but shared by the Canaries with other Macaronesian groups (Azores, Madeiras, Cape Verdes). There are seven principal islands.

<i>Number of Islands.</i>	<i>Number of Species.</i>	<i>%.</i>
One	4	8
Two	9	18
Three	12	24
Four	14	28
Five	6	12
Six	3	6
Seven or more	2	4
	<hr/> 50	<hr/> 100

B.

Distribution in the Canary Islands of *Canarian* endemic species—that is, of species confined to that group as distinct from the Macaronesian endemics which characterize Macaronesia as a whole.

<i>Number of Islands.</i>	<i>Number of Species.</i>	<i>%.</i>
One	248	62
Two	73	18
Three	35	9
Four	28	7
Five	8	2
Six or more	8	2
	<hr/> 400	<hr/> 100

There can, therefore, be no doubt that in the Canaries the endemic species that also occur outside the archipelago in the other Macaronesian groups have a much wider distribution than those restricted to the islands, range in the group going with range in the whole floral region, as Dr. Willis has established for New Zealand. We will now ascertain how botanists have explained the origin of the two kinds of endemic species. In the first place we will deal with the Canarian endemics proper. Hooker had long been interested in the floral history of the group. He gave it a prominent place in his *Lecture on Insular Floras* in 1866, and twelve years later he gave his matured views in the appendix to the joint work by Ball and himself on '*Marocco and the Great Atlas*' (p. 417). For him the endemic species peculiarly Canarian came into being as derivatives of parents of Mediterranean type that reached the islands long ago. 'As an example of the prevailing methods and 'generally accepted views' among systematists in the latter half of last century Hooker's remarks have great importance in connexion with the subject of this paper, and they are here quoted in full:

'The wonderful development in the Canaries of endemic species, belonging for the most part to Mediterranean types, points to the very early

introduction of the parent forms of these, and the long isolation both of the Archipelago and its separate islets. It is in accordance with generally accepted views to assume that the endemic species of each genus have been derived from parent forms originally introduced into one or more of the islets; and that as the descendants of these species spread over the Archipelago they were exposed to different conditions in each islet, resulting in their varying, and in the segregation and conservation of different local varieties each in its own insular birthplace; a supposition which is in accordance with the fact that those endemic species are really very local, many being confined to a single islet.'

But Hooker held quite a different view for the origin of the Macaronesian species, and especially for the most typical of them, those of the Laurel Woods. Whilst regarding the mass of the non-endemic species of the Canaries as Mediterranean plants, and the mass of the true Canarian endemics as derivatives of yet earlier Mediterranean types, he recognized a great break in the floral history of the group when, on taking a step farther back, he came to handle the Macaronesian species. Here he found the wreck of an ancient continental flora which, having been expelled from the continent through secular changes of climate, had 'been preserved in the more equable climate and more protected area of the Atlantic Islands'. This view, which was elaborated in his Lecture in 1866, was restated in his book on Marocco (pp. 417, 419). It was based on the discovery of plants in the Tertiary beds of Southern Europe, closely allied to or identical with living Macaronesian species.

The trend of the later evidence indicates that the Canaries and the Macaronesian groups generally are by no means alone in this respect, and that islands have often been sanctuaries for the survivors of continental floras that have passed away. However this may be, the view of Hooker, that the remains of an extinct European Tertiary flora still survive in the Macaronesian Islands, was combated by Grisebach in his 'Die Vegetation der Erde' (1872), but, as Engler has shown, on quite insufficient grounds. It was strongly supported and extended by Engler himself in his 'Versuch einer Entwicklungsgeschichte der Pflanzenwelt' (1879-82, i. 74), and had in the meanwhile been confirmed by later geological discoveries, notably those of Saporta and Marion (1876). Engler held to the position tenaciously, and remarked that 'even if we do not allow that the existing Macaronesian species are but slightly altered forms of species which lived in Europe in Tertiary times, we have sufficient other grounds for the belief that the endemic Macaronesian flora dates in great part from the Tertiary age and that the insular conditions have contributed to its preservation'. Drude, in his 'Handbuch der Pflanzengeographie' (1890), deals on similar lines with the Tertiary character of a portion of the endemic element of the Canarian flora.

This brings us to another stage in the argument. We now perceive that whilst the species peculiar to and characteristic of the Macaronesian floral region have a much wider range in the Canaries than the purely Canarian endemics, they are also far older. Whilst the Macaronesian plants are remnants of old Tertiary forests of Southern Europe and North Africa, and represent types that have disappeared from the continent, the purely Canarian endemics belong to types still predominant in the Mediterranean region. The Macaronesian endemics are true 'relicts' and are widely spread over the Canarian archipelago; whilst the purely Canarian species are of recent and local origin, and are for the most part limited to single islands. As already implied, the species peculiar to the Canaries are eight times as numerous as the Macaronesian species. The purely Canarian species would, in accordance with the theory of Dr. Willis, be the most liable to extinction, and this finds support in the behaviour of the *Statice* of the subsection *Nobiles* as described by Dr. Stapf ('Annals of Botany', xx, xxii). They are very local and 'there is a considerable risk of their total disappearance'. We should not look for the same with the Macaronesian species. But they must go the way of all plants, and one of them (*Clethra arborea*) has not been found since 1828.

In the more recent Flora of the islands by Pitard and Proust (1908, p. 77) we have important light thrown on the origin of new species in the Canaries. If they had not been following the practice long in vogue among systematists in dealing with insular floras, a practice well illustrated in the quotation from Hooker (already given) when he was discussing the origin of the Canarian endemic species thirty years before, one might have credited the authors with anticipating Dr. Willis in the matter of the Age and Area theory. But, as held by the writer, the real significance of this theory lies in its return to a pre-Darwinian position respecting plant distribution. Dr. Willis has here rendered the greatest service to botanical geography by demonstrating the importance of principles that had been almost forgotten in the efforts to apply the great theory of Darwin to the central problems of the plant world.

Viewed from the standpoint of Age there were for Pitard and Proust two types of endemic species in the Canaries. There were in the first place those found generally distributed over the group, very ancient forms that once existed in the neighbouring continent, but now survive only in the Macaronesian region. (These are the Macaronesian endemics before recognized.) Then there were the much more numerous recent forms, mostly localized in single islands and derived, just as Hooker held, from parent forms already in the archipelago. These are the purely Canarian species, and the authors of this Flora make some very suggestive remarks on Nature's mechanism in their production.

They take the case of the representatives of *Micromeria*, a cosmopolitan

Labiata genus. Of the 20 Canarian species 15 are confined to one island, 3 to two islands, 1 to three islands, and the last, *M. varia*, a highly variable species, abounds all over the group, occurring also in Madeira. They assume that *M. varia* has probable descendants in species restricted to single islands and they extend this position to many other genera. We could not admit (they argue) in the cases of numerous other genera, *Statice*, *Senecio*, *Sonchus*, &c., where this occurs, that the species originally existed in all the islands and died out in all but one. Evidently they hold with Hooker that the single-island species have arisen as adaptations to the particular conditions of individual islands.

We have here spontaneous testimony that the rôle of the polymorphous or highly variable species in the development of new forms, a rôle which is so conspicuous in the later floral history of the islands of the tropical Pacific, is equally well illustrated in the Canaries. The principle is exemplified in its simplest shape in a compact genus or subgenus ranging over an archipelago and holding a score or so of species. Here a solitary highly variable species ranging over all the islands becomes the parent of several localized species that are often confined to single islands. But it is as true of a section of a genus characteristic of one group of islands as it is of a large genus distributed over many archipelagos and holding, as in the case of some genera of the Pacific, an ocean in its sway. It is as true of a subgenus confined to a small continental area as it is of a wide-ranging genus that covers a continent. It is often beautifully illustrated in the behaviour of a single species as a parent of numerous local races and varieties. It was the part taken by the polymorphous species in the Pacific, differentiating in every group and even in the individual islands of a group, that first led the writer to view the world of Nature as in the main a differentiating world. It represented for him in miniature a fundamental principle of distribution. Here on a small scale he recognized the process of the differentiation of the primitive generalized types that once ranged the globe.

The subject was first worked out by the writer in his volume on plant dispersal in the Pacific (1906), and it is there shown how numerous botanists, however much they might differ in other points, were at one in recognizing the play of the polymorphous or highly variable species in that region. The principle is either illustrated or implied in the case of one genus or another in the writings of most of the botanists who were interested in the floras of the Pacific Islands during the latter half of the last century and in the beginning of this, of Bentham, Burkill, Cheeseman, Drake del Castillo, Gray, Hemsley, Hillebrand, Reinecke, Rendle, Seemann, and others. Now we find it recognized in the Atlantic Islands, directly in the pages of Pitard and Proust, and by implication by Hooker for the Canaries in his reference to the 'generally accepted views' respecting the origin of localized endemic species in that group.

But the most significant fact in this connexion is that when Dr. Willis first promulgated his theory of Age and Area ('Ann. Roy. Bot. Gard. Peradenya', May 1907) his preliminary statement of it took this form. When he came to elaborate it he gave it the name of its most striking implication, Age going with Area. He arrived independently at the same conclusion respecting the plant-stocking of Ceylon and the adjacent mainland that botanists a generation ago had framed in the case of genera of the Pacific Islands. We have been apt to forget this preliminary statement of his position; but it is the essence of his theory. His views on the local origin of endemic species were first presented in this form:

'The general principle on which India and Ceylon have been peopled with the many species which they contain would seem to be that one very common species has spread widely; and so to speak shed local endemic species at different points, or else that one species has spread, changing at almost every point into a local endemic species, which has again changed on reaching new localities.' Examples are given of *Clematis* and *Anemone* in the Himalayas (we are told that many more cases could have been cited), where we have associated with a single species ranging throughout the region various allied species confined to particular localities. When Dr. Willis asked how these cases could be explained 'but on the parent and child theory' he put a question which many of us have asked.

But this principle is not merely insular. It is, as we have seen in the case of the Indian mainland, also continental. Whilst the highly variable species may cover much of a continent, its derivative species are restricted to small areas. Few better examples could be given than those of different species of *Geranium* over great areas of the Eurasian steppes, in the highlands of Mexico and Central America, over the length and breadth of the Andine region, and in the high mountains of the breadth of tropical Africa. The rôle of the wide-ranging polymorphous species, as a parent of localized endemic forms, has been as effective in the great mountainous regions of the continents as it has been over the archipelagos that dot the oceans. (As concerns *Geranium* the subject is lucidly treated by Knuth in his monograph on the Geraniaceae, 1912, one of the Pflanzenreich Series, pp. 79, 83, 85, 175, 185, 196, 202.)

It may be remarked in conclusion that of the several eminent botanists cited above not one could have been cognizant of any such theory as that of Dr. Willis. They have been named here in connexion with the important part played by the highly variable wide-ranging species in distribution, and it is on the behaviour of these polymorphous species that Dr. Willis based the preliminary statement of his views on the local origin of endemic species. His principle was often implied in the practice of these systematists, though not as an integral principle, but as part of a code that was none the less valuable because it was often unwritten. In theory a few

were Darwinian evolutionists, but many were not. The last, subordinating their theory to their practice, were, as I am willing to believe, 'differentiationists' at heart, holding, like their predecessors, ideâs of divergence or differentiation of types, but ideas admittedly crude, and such as Hooker held in the shape of 'Centrifugal Variation' through much of his career. In their theory, as I take it, they followed Nature on her broadest lines, and they did their best to put it into their practice. This is the position to which the Age and Area theory will bring us back, a position that has been for a long while greatly obscured by the clouds of dust that have been raised in the Darwinian controversies. It is certain that this theory will be involved in a general differentiation hypothesis of some kind. Whether that position will be provisional or permanent, time will show. At all events the two views of Differentiation and of Age and Area seem to be inextricably bound together now.

List of the Macaronesian Species of Flowering Plants in the Canary Islands, being those also found in other Groups of the Macaronesian Floral Region (Azores, Madeiras, Cape Verdes), but not known outside it.

The letters after the names signify as follows: A = Azores; M = Madeira; V = Cape Verdes.

The arrangement adopted by Christ has been followed.

Ranunculus cortusaefolius. M.	Sempervivum (Aichryson) radicescens. M.
Dichroanthus mutabilis. M	Bencomia caudata. M.
Lobularia intermedia. V.	Cytisus stenopetalus. V.
Fumaria montana. V.	Jasminum odoratissimum (barrelieri). M.
Laurus canariensis. A, M.	Picconia excelsa. A, M.
Phoebe barbusana. M.	Heberdenia excelsa. M.
Persea indica. A, M.	Clethra arborea. M. ¹
Oreodaphne foetens. M.	Echium stenosphon. V.
Hypericum (Androsaemum) grandiflorum. M.	„ candidans. M.
„ glandulosum. M.	Campylanthus salsoloides. V.
„ floribundum. M.	Lavandula pinnata. M.
Visnea mocanera. M.	Micromeria varia. M.
Geranium anemonaefolium. M.	Cedronella canariensis. M.
Ilex canariensis. A (?), M.	Leucophaea massoniana. M.
Rhamnus glandulosa. A (?), M.	Teucrium (Poliodendron) heterophyllum. M.
Euphorbia mellifera. A (?), M (?).	
Bupleurum salicifolium. M.	

¹ Not found in the Canaries since 1828.

<i>Globularia salicina.</i> M.	<i>Urtica morifolia.</i> M.
<i>Statice pectinata.</i> V.	<i>Myrica faya.</i> A, M.
<i>Phyllis nobla.</i> M.*	<i>Dracunculus canariensis.</i> M.
<i>Viburnum</i> sp. A, M. ¹	<i>Tamus edulis.</i> M.
<i>Carlina salicifolia.</i> M.	<i>Ruscus (Semele) androgynus.</i> M.
<i>Andryala cheiranthifolia.</i> M.	<i>Smilax canariensis.</i> A, M.
<i>Sonchus pinnatus.</i> M.	<i>Asparagus scoparius.</i> M, V.
<i>Beta procumbens.</i> V.	<i>Dracaena draco.</i> M, V.
<i>Rumex maderensis.</i> M.	

Note on the List of Macaronesian Species.

We are far from having done with the matter when we divide the endemic species of this group into those of the floral region (Macaronesian) and those peculiarly Canarian. Almost all the great problems in the plant-story of the region are involved in the list just given. They require a lengthy general discussion, and that being here impracticable we must be content with a bare list. Few of such lists are, however, available; and although this one cannot claim to be free from error, for botanists have made the Canarian one of the most difficult of insular floras, the writer believes that it will give a reliable preliminary notion of the general facies of a very interesting little gathering of plants. The short list bristles with implications, although for several reasons, one of which is given below, we have always to look outside the list to push them home.

Here we must limit the discussion to two of many curious points that arise as soon as we take the list in our hands. A genus originally represented by one or two species ranging over the floral region and by several species restricted to individual groups would ultimately, as differentiation proceeded, be only represented by species confined to single groups. For this reason it will be apparent that some of the most interesting genera of the Canarian flora will be absent from the list of Macaronesian species, their original wide-ranging species having disappeared in the differentiating process. For instance, of the four American genera, *Bowlesia*, *Bystropogon*, *Cedronella*, and *Clethra*, the third is the only one that strictly speaking ought to figure in the list. It is true that *Clethra arborea* is included, but it has not been found in the Canaries since 1828.

Another matter to be here noticed is the inclusion of the Cape Verde group in the Macaronesian region. For the best part of a century this has been a moot point, and it still remains so. In a physical sense these islands have been far more 'africanized' than those of the northern groups.

¹ There are indications that the Macaronesian forms of *Viburnum* are more allied to each other than to any continental plant, such as *V. tinus*.

The great climatic revolution that overwhelmed Northern Africa destroyed the old Tertiary continental forests of this archipelago. The only connexions with the northern groups that we should look for here would belong to what Christ terms 'xerothermic' types that are usually North African and Mediterranean in their range. This is pretty much what we find; but we cannot exclude these islands from the floral region. They must have belonged to it in the past, and they belong to it now, but in a limited sense. They come into it on a lower grade, and must be correlated with the lower or African zone of the Canaries and Madeira, both in a climatic and in a floristic sense. But the connexion with the northern groups, as Christ points out, is not merely a matter of identity of species. It is also concerned with affinity. There are a score or so of species nearly related to Canarian and Madeiran plants and of similar 'xerothermic' types (Hooker in his Lecture, p. 16, takes a similar view).

In framing the above list the works before named of Pitard and Proust and of Christ have been mainly used. But other sources of information have been consulted, such as Schmidt's 'Cap Verdische Flora', 1852; Coutinho's 'Catalogus Herbarii Gorgonei', 1914-15; Watson in Godman's 'Azores', 1870; Trelease on the Azores in the 8th Report of the Missouri Botanical Garden, 1897; and Lowe's 'Manual of the Flora of Madeira', 1857.

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