

An essay on the biogeographic thinking of J. C. Willis

(WITH TWO TEXT-FIGURES)

But a short time ago a distinguished student of plant-life wrote me that few works has impressed him more yet convinced him less than Willis' much rumoured « Age and Area ». Handed down quite passingly this opinion caught my eye rather better than so, for it vividly reminded me that I had felt the very same when reading those pages. Thinking about my first impression rather often during the long years I next on happened to devote to enquiries into dispersal, I gave myself reason by degrees, of course, why the ideas of the egregious British botanist elicit markedly contrasting reactions so fully and so easily.

It is my immediate purpose to write out the explanation which seems to me valid as concerns reactions of the kind and their background. Apparently largely ignored today, still Willis is a powerful influence in the field of phytogeography and botany, even, if less directly, in that of zoogeography. The informed naturalist knows for certain that authors who do not refer to Willis at all still do move within the shadow of this or that particular point of his doctrine. This would not be possible if what Willis once broadcast were not at the same time caducous and lasting, what is lasting of it offering somehow better than passing significance. The work of a figure of this importance should not be ignored or misconstrued much as it may be difficult to find out its mainsprings.

It does not seem necessary that I present for my purpose a full-fledged historical review of the development, and of every aspect of

essential a new approach to basic issues in dispersal only in the light of perfectly outworn tenets of « phytogeography » and « evolution ». Thus gravely handicapped, these censors rested their case on certain errors of Willis, but they never proved equal meantime to the task of reaching the core of his thought. Bewildered they were these critics, and even more bewildered they left their hearers and readers.

As a purely human document, Willis' effort could, at bottom, best be classified in quality of a revolt against Darwin's understanding of « geographic distribution ». Inasmuch as a « geographic distribution » — however conceived — does call into question two of the three essential factors responsible for evolution, that is, time and space (the third factor being form) by challenging Darwin on grounds of dispersal Willis effectively challenged him in point of evolution much in general. Willis does himself underscore this revolt (see, e.g., *op. cit.*, p. 95), and shows that it is the realization that Darwin had erred which forced him to develop his own thinking quite independently. I am rather sure that those of the readers and students of Willis' work who fail carefully to consider the nature of it as a whole, thus to grasp the conflict out of which it sprang, miss an altogether relevant factor of judgement, and because of this I underscore here the circumstance and its necessarily vast scope in many directions, directly as well as indirectly.

The circumstance in question, and so the starting point of Willis' thinking, is of course altogether familiar to me for the very simple, altogether human, and quite scientific reason that I had the same experience in regard of Darwinian « geographic distribution » and whatever « phytogeographic » and « zoogeographic » doctrines stem ultimately from it. It does not seem impossible that I show in detail in a work of major scope just now out of press ⁽¹⁾, that Darwin's « geographic distribution » is unworkable and that whatever « zoogeography », « phytogeography », « New Systematics », etc., are ultimately made to rest on its main premises fall short of answering even the minimal requirements of the biological sciences. To this very extent, and quite independently, I did reach Willis' own conclusion, which means that I possibly understand his main position, whatever I may think of Willis' argument in much detail. He who thus approaches Willis is on the way, I believe,

(1) CROIZAT L. - Panbiogeography, or an Introductory Synthesis of Zoogeography, Phytogeography, and Geology; with notes on evolution, systematics, ecology, anthropology, etc.; 3 vols. of about 2700 pages, and about 300 text-figures. 1958.

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penury, and among these facts some are that hardly lend themselves to different constructions on account of their immediately positive nature.

Let us accordingly try at least to find the grounds common in substance to the thinking of students who, like Willis and myself, are dissatisfied with Darwinian « geographic distribution » and its byproducts. Knowing something of these grounds the reader of this article may without risk of doing injustice to any party in the game eventually conclude whether Willis, and I, were or not in the right when rejecting that « distribution » as the first step toward replacing it with something else. Even more, I will here state outright my own side of the matter by which a comparison will be made easy among what Darwin broadcast, Willis taught, and I happen myself actively to believe.

The attached Fig. 1 does represent the dispersal of the woodpecker (*Aves, Piciformes*) *Dendrocopos*, a bird to which I have often referred in my work (see *Panbiogeography*; Zoological Indices under *Dendrocopos*) because of its outstanding pedagogical significance. The map speaks for itself, the whole way between Tanganyka and Patagonia across the whole of Eurasia and the Americas, nor there is possible question as to what it essentially stands for in science. Some are who will maintain that *Dendrocopos* originated as a certain « species » in e.g., Patagonia, or Tanganyka, or India, which « species » by a series of successful « jumps » and « sweepstakes » managed eventually to reach Patagonia out of Tanganyka or Tanganyka out of Patagonia, and the merry like; but many more will be who do not believe that in the very least on the self-explanatory ground that it is absurd by time and by space alike. It *must* be absurd for, were it not absurd in regard of *Dendrocopos*, it should be true in regard of the whole of life comparably distributed, and in the end of life all over. Were it not absurd, the whole of life would be doing nothing but jumping from Tanganyka to Patagonia, and the merry like, for no better reason than « origins », « casual means », « sweepstakes », « tempo and mode in evolution » do impel it that way. This might be science but not many. I am certain, will agree that it is truly science unless better supported than by affirmations that Darwin said it, Wallace maintained it, Mayr claims it, Simpson is sure of it, Darlington Jr. dotes on it, etc.

As a matter of fact, the hypothesis of « casual means », « jumps », « sweepstakes » — whatever, in a word, is « zoogeography » today — comes to irreparable grief before a pattern of distribution the like

Dendrocopos. True in this to the standards set by the whole of the Piciformes (that is, by a massive sector of avian life), *Dendrocopos* steers entirely clear of Madagascar and Australasia. Much as I have asked my good friends, the « zoogeographer » and the « phytogeographer », how they would explain a limitation of this peculiar sort I have never found any of them willing to answer my invitation with some precise, pointed statement of documentable reason. They have told me, of course, that there stands some « filter-bridge » between Tanganyka and Madagascar, etc., but they have never been competent to go farther than to claim it, not to explain why, active in regard of, e.g., *Dendrocopos* still this « filter-bridge » would allow iguanid lizards of evident American type to reach Madagascar, while at the same time keeping out of Madagascar agamid lizards of manifest African and Oriental description. Curious, is it not? ⁽¹⁾.

Quite as striking, and inexplicable the « zoogeographic » and « phytogeographic » way, is the well authenticated fact that altogether precise vicariism in space is established in Northern Corea between two species of *Dendrocopos*, *minor* and *canicapillus*, which otherwise range the full way between the British Isles and Western Malaysia. How really « casual » is dispersal of this utmost precise kind, in space and so necessarily in time, is a question that the reader may ask the « zoogeographer » and the « phytogeographer » among his friends to explain, of course, this time, with solid reasons and documentable facts to support.

Finally, and against the very core of the Darwinian « geographic distribution », its « origin of species », « center of origins », « means of transportation », etc. — that is, the whole of current « zoogeography » — stands the essential consideration that *Dendrocopos* does consist between

⁽¹⁾ The subject mentioned, but not referred immediately to a source in this paper, are amply discussed in my *Panbiogeography*, to which I implicitly refer the reader. I much regret, of course, that I cannot follow the matter up at greater length here. The attentive reader should not fail to pay attention for example to the massive disconnection that has place in *Dendrocopos*' ranks between Western Panama and Southeastern Bolivia. This disconnection is altogether standard by plants and animals, and is fundamentally involved with the whole of a pale of dispersal (i.e., forma-making and translation in space as one) that interests the Eastern Pacific, therefore also Galapagos most intimately. The fern *Doryopteris pedata* (see *Panbiogeography*, Vol. I, Fig. 119D, p. 926; also Fig. 109, p. 776. For a desultory discussion of the distribution of this same plant refer to Tryon, R.M. Jr., in *Amer. Jour. Bot.* 31: 470 (1944) exhibits distribution of this type clearcut, though the disconnection it presents is somewhat shorter by mileage than the one displayed by *Dendrocopos*.

course a good, long look at Fig. 1 again — is wholly free to dissent in the name of whatever may strike him as erroneous in my viewpoint using for the purpose the fullest brunt of current « zoogeography » — its « centers of origin », « casual migrations », « sweepstakes », etc. — thus hopefully to prove false whatever I state. I am for my part rather sure right here that the reader will have a particularly hard time meeting the challenge of the facts summarily expressed by Fig. 1 if making for the purpose implicit and explicit recourse to the notions of the Darwinian « geographic distribution », and to the « zoogeography » which immediately stems from it. I do not thus fling a wanton challenge because I have tried for longer than a quarter century to work out these skeins to their best end, first one way, then another way, etc., always coming to the conclusion — and so against the background of a mass of evidence to cover rather more than the 3200 pages I have finally given to print — that what I have proposed above is the lone way out of difficulties otherwise not to be mastered. Since the way-out in question is essentially simple — childishly simple in reality —, quite logical, and of easy application to every case of life I should believe that it is at least as close to the truth as man may have it just now. Of course, what the Almighty would say of it I do not know, but what man may eventually think of it is not a question I have allowed to go wholly unheeded over the years. If, as the Holy Writ maintains, God made man unto His likeness it is at least probable that a science of dispersal is understood in heavens rather not in the way in which Darwin and his followers have understood it from 1859 to this very day.

So far with *Dendrocopos*, and what thus does here immediately interest the zoologist. As to the botanist, he may turn to Fig. 2 which illustrates this time the main trends of the dispersal of genus *Euphorbia*. The caption will supply essential information, and so I may here freely turn to a minimum of general considerations.

It is very easy, and not at all risky, to identify two main factors active in the evolution of this truly stupendous genus, as follows: i) The genus as a whole, that is, understood *sensu latissimo*, and its allies within the Euphorbieae as well, are characterised by a most peculiar reduced inflorescence simulating a flower. This inflorescence (*cyathium*) consists of a central female flower reduced to minimum essential (i.e., an ovary) surrounded by clusters of male flowers (also reduced to their ultimate expression, i.e., a stamen), the whole contained

within an involucre suggesting a calyx and bearing glands reminiscent of fleshy petals. Fairly actinomorphic in certain genera (e.g., *Euphorbia*, *Neoguillauminia*), the cyathium is more or less openly zygomorphic in certain others (e.g., *Pedilanthus*, *Anthostema*, *Monadenium*, etc.); ii) Forms uniformly provided with a cyathium in the sense of *Euphorbia* exhibit differences in e.g., the glands (appendaged or not, etc.), their arrangement (discrete or continuous, etc.), and in the like, without for this the basic premises of the cyathium altering, as such, in any material way. However, the somatic parts of these same forms do greatly vary in nearly everything of foliation, spinescence, duration, gross anatomy, etc., the exactions by different environments being met in turn by succulence, rapid cycles of growth, abortion and reduction of the main axis, etc.; iii) In view of the preceding, it seems certain that there is in *Euphorbia* a firm long-range tendency toward establishing a definite type of inflorescence in obedience to a still more generalized tendency (see, e.g., *Dalechampia*, *Pera*, etc.) toward a reduction and adaptation in general of all floral parts. This stands as a matter of fact as the basic tendency responsible for the Euphorbiaceae as a distinct family of their own, and can in no sense be viewed as adaptive, whatever the concept we may form of « natural selection », « adaptation » to particular needs or to climate, etc. There is in *Euphorbia* likewise a tendency to modify the somatic body in immediate answer this time to the environment, as when, for example, extreme succulence (e.g., *E. obesa*) is developed to meet the rigours of xerophily of a pronounced character. However, even under comparable conditions of extreme xerophily succulence may be developed of a different kind (e.g., *E. lignosa*), and tuberization mainly for storage-purpose may be secured under or above ground amid very different climatic conditions (e.g., *E. rapulum* and *E. caput-medusae*). To a point, the tendency bespoken by somatic changes of the kind may be understood as due this time to « natural selection ».

Summing up and concluding: The evolution of *Euphorbia* has marched on throughout the ages in answer to main tendencies and to particular adaptations as one, the former being in the long run the more important for, had they not been orthogenetically present, a group like *Euphorbia* (surely more than a 1000 conservative species) could not keep together, but would have frittered away through time and in space into endless petty segregates, each having a different type

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conservative estimate. The tendency responsible for the coarctate inflorescence of *Dalechampia* and *Euphorbia* as one is certainly quite older).

Succulent cacti and euphorbias do consort at very few points of the map (e.g., Yucatán, Eastern Brazil, the coasts of Tropical Africa, Ceylon), the former inhabiting the New World (with the exception of *Rhipsalis* in Tropical Africa and Ceylon), the latter the Old World (with the exception of certain forms as, e.g., *E. pteroneura* in Tropical America). There is of course no possible way of accounting for distribution of this neatly vicariant type (a vicariism duplicated by, e.g., *Agave* and *Aloe*) unless under the hypothesis that the main massings of Cactaceae and succulent *Euphorbia* were established *in origin* to cover the one the New, the other the Old World. Likewise, the existence of large crops of species answering a common « type » (e.g., the « *Treisia* » of South Africa; the huge candelabrifform species scattered along the Great Rift of Africa, etc.) proves that ancestral forms rich in genetic potential for the gradual release of swarms of eventually new forms of the specific and subgeneric order had age-long prior localization, too. Concluding, a concept of *main massing*, and a concept of *genetic powers* are necessary — against a notion of « casual means », « chance dispersal », « sweepstakes » and the opinionate like — to an understanding of the facts and circumstances we are reviewing here quite so briefly.

I have of course no quarrel — not at least before the deed — with anyone who may think of convincing me that in order to understand the dispersal of *Euphorbia* I am bound to identify the « origin of (a certain) species », in order eventually to have said « species » flying through the airs between Capetown and Krasnoyarsk in the teeth of « casual means of transportation », whether « endozoic » or « epizoic », and the like again. I should however earnestly advise the gentleman not to lose his time in schemes of the kind, rather, to lay hand upon the records of the distribution of *Euphorbia* in particular, and of life much in general, jotting down on the map of the world the score of their occurrence, next to compare as many different patterns of distribution as possible in order thus efficiently to learn what they bespeak as a *factual whole* after all. Quite as in the case of *Dendrocopos*, the various forms of the Euphorbiaceae, Euphorbieae, *Euphorbia*, etc., gradually and vicariously developed through time in space, each aggregate out of a group in an earlier state of evolution and so with more generalised cha-

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work within the sundry groups of species, and the requirements of the environment will interlockingly promote change, with the result that in the end — by very slow, gradual averages overall — differences today, e.g., of the subgeneric order will mature as fully generic into the future. In the end to a new geography, physiography, ecology, etc., shall correspond a new form-making, a new distribution, a new biology, etc., flesh and rocks altering together through an endless chain of past becoming present and yet to become future, step by step, there never occurring a break really to count between what was and what will be. In sum, *time and space and form shall forever stand as one orderly triad*; and he who is to misunderstand the first two — as Darwin did, and the modern « zoogeographer » and « phytogeographers » with him do — will never achieve an understanding worth the name of the last; therefore, shall in the end not understand evolution to the full.

When we speak — the reader may carefully note — of a distal ancestor with the genetic potential qualified to sire *Dendrocopos*, *Dendropicos*, *Picoides*, etc., as finally distinct « modern » genera; or we visualize a quite as distal ancestor having characters apt eventually to mature by ultimate recombination as the « modern » genera *Euphorbia*, *Pedilanthus*, *Anthostema*, etc.; and we credit these ancestors with dispersal over the continents as the necessary prelude of the intercontinental distribution of their « modern » descendants; we do of course hypothesize nothing that is theoretical or controversial. We do as a matter of plain fact assume precisely the very same state of affairs that factually belongs today to *Dendrocopos* and to *Euphorbia*, both of which are today *already distributed* on a vast intercontinental scale as a prelude — everything being equal — of quite as vast a pale of dispersal eventually to be held by the forms to arise out of their bosom into time through space by averages and degrees. Should the reader not be particularly interested in *Dendrocopos* and *Euphorbia* let him by all means bring into play, e. g., *Phyllodactylus* and *Senecio*, *Danais* and *Pinus*, etc., in the understanding that he will change subjects but he will certainly not get out of the power of the laws which rule all these subjects alike through time in space. In brief, form is a « specialised subject » in a narrow sense all right, but time and space are themselves the matrix within which every form eventually comes to its rest, and a science of dispersal must have time and space as its own, if it is to be a true science of dispersal at all. Judged in this light — the legitimacy

sought not so much in what I think of the doctrines which he rightly intended to destroy as in what I think of the ways and means by which he tried to replace them with something better.

That Willis did revolt against Darwinian «geographic distribution», consequently also against practically everything of Darwinism in the long run is, to repeat, something for which he can only be warmly praised. He would have known less, and be less of a man if, satisfied that «natural selection» did not explain the why and the how of the plant-life of Ceylon, he would have meekly submitted in the name of the reason that, after all, practically everybody would be against him. His attitude can accordingly only be viewed as gentlemanly and scientifically correct as a matter of principle.

However, the question we face is by no means settled with this. The question with us here is what did Willis replace Darwinism with; and facing it the objective enquirer is bound, alas, to report that Willis did replace Darwinism with a queer mixture of theory amounting to an attempt of «out-darwinize» Darwinism, therefore basically non-viable, also with certain exceedingly shrewd tenets and guesses. In sum, the student of *Willisiana* finds in its pages two contrasting matters: one as the byproduct of inductive theorizing in the obviously Darwinian tradition, and so no more successful than anything which Darwin and his followers ever devised along the slippery path of assumption; the other representing on the contrary solid knowledge of the factual kind out of the stores of a man who had had ample opportunity for studying botany quite as much in the cabinet as in the field.

Anyone deeply sympathizing and feeling with Willis as to the latter can but regret that Willis also dealt in the former; and so he will readily understand the reason why those who study the works of the egregious British botanist are attracted and repelled in even measure. It is not their fault at all. It is Willis' own, who ran two hares at the same time. The very core of «Age and Area» is an attempt to deal with the «origin of species» in a manner but on the surface other than Darwin's therefore nothing that ever could be more successful in the end than Darwin's own distributional schemes.

I see no difficulty in polarizing what I think on the score concentrating precisely on certain main aspects of Willis' thought wherein the roots of his ultimate failure are, as I understand it, quite clear for everybody to see.

future, — again around local centers of form-making — for races and species to come in which shall be recast in different degree of combinations the characters belonging today to the living forms. Because of this, evolution necessarily proceeds from larger to smaller divisions, that is, from top down, once again quite as Willis maintained.

I stress form-making taking place around essentially local centers, as when for example the different peaks of a single mountain chain do harbour vicariant races, or species arise, somehow, in particularly local isolation. It is of course true that against these quite sharply localized forms there stand opposed other attuned to laxer biology and ecology (e.g., the arid « parklands » stretching along the slopes of an Andean chain), therefore by far more widely spread and dispersed. However different the details, it seems nevertheless to be rather plain that the ultimate manner of form-making of the ones and the others cannot be substantially different, therefore, that it is by far the better advice concretely to work to find out what the origins of all these forms exhibit which is common than to labour at first to underscore the pettiest of their differences. Whatever the case, and freely granting that similarities and dissimilarities are equally important to science, a study of the subject, if properly conducted, cannot begin with *inductive* theorizing but with a *deductive* enquiry into the records of life themselves.

Unlike Darwin who visualized hypothetical « center of origin » and « origin of species » toying in the process with the question how many live grains could be contained in the gizzard of a pigeon slain by a hawk and the like, Willis had, as we just heard, proper appreciation of the basic mechanism of translation and form-making in space and through time, which mechanism has its roots precisely in the essential course of evolution. He none the less thoroughly understood (op. cit., p. 1) that the ultimate task of a science of dispersal would be in disposing of the question why, how, where, and when did all the forms of life arise, and why, whence, and when did they move to reach the sundry spots where they live today. Willis had in other words the coordinates fully mapped before himself and the knowledge required in essentials to dissect Darwinism to its very core and, in particular, to replace Darwinian « geographic distribution » with something vastly better. To perfect the task he but should present the learned world with a detailed account of what life, plants and animals, itself demonstrates through its records, for or against Darwin and everybody else that it

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what is true of a certain bird, frog, or daisy is no longer true of a certain other bird, frog, or daisy. This being the case, the informed inquirer is of course warned by life's own scores not to tarry on what of life is fleeting and casual in point of detail, therefore both true and false depending as to the subject immediately under consideration. The informed inquirer will drive on the contrary after principles of ultimately broader scope and significance; the principles that are either true or false in function of the whole of the facts.

Willis, however, would not here feel with me. In his mind, the pre-Darwinian tenet that the species were created for the localities where they now occur was necessarily better. Having once observed — which purely as a fact may be well established, and I would at any rate accept as probably true if affirmed by an observer of Willis' ability — that the most widely distributed species of the Ceylonese flora (*Age and Area*, p. 60, *op. cit.*, p. 13) are the ones, which on the average, spread beyond Peninsular India while the least widely distributed in Ceylon happen to be narrowly endemic to Ceylon, he rushed rather inductively to the conclusion (*op. cit.*, p. 16) that, within their own circle of affinity, and on the average, the most widely dispersed plants are the oldest, the less so the youngest.

I do not see the cogency, even less the necessity of this conclusion, and I can only deeply regret that an author who had so happily begun would so lightly formulate it. It is at any rate most unfortunate that the name of Willis stands today associated with a brainstorm of the kind, and that because of this the solid contribution he made otherwise to science hardly receives full consideration. Insofar as I may speak for myself, I never have felt any need for something like Willis' theory of « Age and Area » in all my work, and had I ever reached the conclusion that something like it would, after all, serve an even partly constructive purpose, still I would never think of tying « age » with « area » in the Willisian manner. In the very first place, the age of a species is exceedingly difficult to determine if at all ascertainable, for the very elementary reason that whatever one may try to conclude on its score cannot be formulated unless having regard to particular cases, case by case, not at all as a general statement. In my opinion, a responsible approach to life and its problems demands extreme flexibility of handling sequentially associated with quite as extreme rigidity of interpretation whenever fundamentals are really in question. However

considerations on « Age and Area » but a very great deal to do instead with something else vastly more pervasive and profound by time and over space; something by which the Deccan rather than the Himalayas, Malacca rather than Burma, etc., stand bound to Ceylon whether by bird or by plant. *Deductively* tested against an adequate basis of approach, the bios of Ceylon would yield intelligence to prove that, in sum, « Age and Area » could in no sense be a primary consideration though they might, perhaps, be an interesting secondary one. Even more, so conducted, the enquiry would of course dispose of the myth spun around a certain « natural selection » without for this enthroning in its place the other myth of some « age and area ».

Why Willis who, to repeat, had enormous botanical knowledge failed to see this, while scattering at the other hand lavish evidence of sober thinking on every aspect of dispersal and evolution throughout his work, is a question that ordinary rules of logics cannot explain. Something irrational is here clearly in play which, acting in regard of a being otherwise so rational as Willis, must hinge somewhere on the appearances at least of sober logics. In other words: What is the correct premise which Willis placed at the very base of his incorrect theory? This is not a wholly academic question for it may, if properly answered, help us in the task of appreciating where, and to what degree, is that theory finally and absolutely objectionable, and so what use we can make of Willis' work beyond the purview of some more or less fortunate claim.

My explanation is of course returned for whatever it may be worth, but the probability is overall that it comes as near to the core of the matter as anything so far contributed to *Willisiana*. If not, it may at least give some preliminary account why the work of the learned British botanist has invited reactions so extreme and so contradictory.

As we heard, Willis had a clear perception of the essential mechanism of evolution (or form-making, that we had better call it here) upward and downward. Knowing as he did that four modern species A, B, C, D do essentially stand for locally effected segregation out of the ranks of an older groups of populations A', the British botanist would quite readily — and so by far not without reason *in theory* — conclude that, e.g., D is necessarily younger than A', and that it would take it time eventually to range beyond the narrow initial sphere of its immediate form-making as « modern species » D. To this very extent,

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in spite of what Willis' theorizing might infer to the contrary from its localization.

Old and beyond question relictual, this primrose could yet spread beyond its present distributional compass if, of course, suitable habitats were created for it beyond the sphere of its present occupancy. Assuming that physiographic and geologic change would intervene to reconstruct, for example, parts of the ancient « Tyrrhenis » out of the bosom of the present day's sea, *P. palinuri* surely might overrun them. Indeed, the process to achieve this would require no change on the part of the usual *means of survival* of this perennial, because these means would be turned into *means of dispersal* by nothing more than the environment suitable for ecesis enlarging by fast or slow steps that they be. Once widespread, *P. palinuri* might be disassembled by further change into sets of separate populations and — *genetic powers for further form-making being still available!* — yield a crop of new varieties eventually to become new species, etc.

So simple an example as this primrose proves in my opinion that:
i) At some very distant time in the past a certain group of *Primula* widespread among Ethiopia, the Pamirs, the Eastern Mediterranean, and the United States yielded by local differential form-making subordinate entities in Ethiopia, the Sinai, « Tyrrhenis », Northwestern India, Montana, etc. Each one of these subordinate entities was necessarily younger by age and held less area than the whole of the ancestral populations; *ii)* *As of today*, however, the « modern » species *P. palinuri* can in no sense be viewed as « young », and it is immediately repugnant to sober reason that theoretical postulates, whether by Willis or somebody else, try to maintain the contrary by playing upon « age » and « area » in an inductive approach to nature; *iii)* Whether « young » or « old », widespread or just the contrary, a species like *P. palinuri* could gain ground, or on the contrary become fully extinct depending upon further geologic, physiographic, ecologic change; *iv)* Whatever its age, and to a large extent its localization, a species like *P. palinuri* could break apart, given the right conditions, into isolate populations and — *time and genetic powers being still available* — become the fountainhead of form-making renewed into the proximal and distal future.

If the reader does try to meet all these contingencies with « Age and Area » postulates he may only conclude in the end, that while

is hardly original with me because I can thank Willis himself for it most immediately. When for example he practically forgets his own theories, and coldly analyzes the flora of islands (op. cit., p. 464 *et seq.*) he returns data and thoughts of unquestionably high significance. The 236 theses that stand as his « General Conclusions » (op. cit., p. 489) are, as I have remarked once before, largely excellent, and furnish at any rate a body of thought and suggestion of challenging value and scope. I am satisfied as a matter of fact that anyone laying hands upon Willis' theses and comparing them with the conclusions reached in my own work will without much difficulty establish concordances of interest for the whole of a science of evolution and dispersal. I have not copied Willis, nor has he borrowed from me, but on the ground that we have both paid living nature perhaps better than passing attention we have inevitably reached in many respects conclusions to match. It is not impossible that my own work is essentially original, and that it may as such finally impress the majority of its readers and users. However, were this work to be « placed » somewhere in the stream of our times anyhow, it surely would not fall with Darwinism in the least (and even less with Matthewism, Mayrism, Simpsonism, Darlingtonism, Goodism, etc.) but find more or less distal place in the sphere of Willism. This conclusion does of course not authorize the codicil that I am a firm believer in « Age and Area ».

That the work of Willis would elicit contrasting, at times downright violent emotions and reactions is of course understandable, quite it is understandable that the nerves of the discriminating lover of music would at different times be jangled and soothed by the motives of a symphony composed by somebody who being in no sense a « duffer » still lightly passes from music of very high order to polyphony and outright cacophony. What to do with his output if not dutifully register for the phonograph whatever of it is worthwhile (and this is surely much), while at the same time throwing the rest out of the window into lasting oblivion?