of oogenesis, spermatogenesis, fertilization and embryogeny, have been described rather thoroughly in some forms and have been outlined in others. The swimming sperm, a fern character, is still retained by all the living genera; but the development of the archegonium is more advanced than in *Pinus*. The embryogeny is more primitive than in any known forms of the Coniferophyte phylum. While these features are of great importance in deciding the interrelationships of the living genera, they could not have much value in determining the origin of the cycads, unless we could learn corresponding details of Mesozoic and Paleozoic forms. What some of these details must have been, we can hazard a guess. The seeds of the living cycads are large, some of them reaching six centimeters in length. In such a seed, the female gametophyte is large, with large archegonia, the pollen tubes are long and there is an extensive free nuclear period in the embryogeny. No Mesozoic seeds in either Cycadales or the Bennettitales even approached the size of the seeds of some species of *Cycas* and *Macrozamia*. Consequently the female gametophyte must have been smaller, with smaller archegonia and probably a shorter free nuclear period in the embryogeny. The pollen tube must have been shorter and may have contained many sperms. In the Bennettitales, with their very small seeds, the female gametophyte must have been very small, with little free nuclear division, extremely small archegonia and, perhaps, no free nuclear stage in the embryo. Pollen tubes were either very short or entirely lacking. In the Paleozoic Cycadofilicales, with many of the seeds smaller than those of the Bennettitales, there were no pollen tubes, and in the earliest seeds the conditions could not have been much more advanced than in some of the living species of *Selaginella*. While these structures may seem visionary, they are about what we should expect to find, as we go from large seeds to smaller and smaller ones, if the same kind of differences which we see in the larger and smaller seeds of the living cycads are continued in the still smaller and smaller seeds of the Mesozoic and Paleozoic forms of the same phylum.

While we believe that microscopic details, if available, would be of even greater value than the macroscopic in tracing relationships, we feel certain that the facts already known prove that the Cycadales have come from the Cycadofilicales and that the differentiation of the two groups may have occurred long before the end of the Carboniferous.

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"AGE AND AREA" IN RELATION TO EXTINCTION

THERE are few generalizations in regard to the geographical distribution of species which have aroused so much interest and elicited so much criticism as the theory of Age and Area of Dr. J. C. Willis. I think it must be admitted that the laborious statistical researches of this investigator have established a fairly definite relation between the number of related endemic species in a given region and the areas which the several species occupy. Willis finds that species of wide distribution are relatively few in number; species whose range is less wide are more numerous, and species which are much restricted in area are most numerous of all. According to the Age and Area theory the "wides" are on the average the oldest species, the small area species being in general those of recent origin which have not had time to spread widely. Dr. Willis believes that under normal conditions species extend their range very slowly, and hence if a species has a wide distribution it must have been in existence for a great length of time. In a very broad and general way this contention is probably right. It is not entirely evident, however, that the species of narrow range are nearly all young, although Dr. Willis has advanced many arguments against the common view that they are species approaching extinction. In general, and so far as is permitted by barriers, the range of a species, according to Willis, is determined not by natural selection or any other agency making for adaptation, but in a more or less "mechanical" way as the result of mere age. "The real difference," he tells us, "between the old view of dispersal and that given by Age and Area is that under the latter we regard *almost all* species as in process of extending their areas of dispersal, not some as extending their areas and as many or more contracting theirs. The exceptions to this—the real relics —are comparatively few and far between, forming perhaps 1 to 2 per cent. of the total of species of very restricted area."[1]

The idea that species are almost all on the spread, and that the process of extension goes on in a "mechanical" fashion leads Willis to set little store by the struggle for existence and selective survival as factors in the distribution of life. "The struggle for existence," he tells us, "can no longer be regarded as an important determining cause in evolution." It acts most strongly in species that are "just commencing." "If they can not succeed in this first struggle they will simply die out and leave no trace. But if they do succeed, they may be looked upon as estab-

[1] "Age and Area," Cambridge, 1922.

lished, for they will be very liable to sudden extermination whether ideally or badly equipped for life."

I am not concerned now with this somewhat curious way of looking at the struggle for existence. Dr. Willis draws rather far-reaching conclusions in regard to the potency of natural selection as a result of his views on the relationship of area of distribution to age. He has established certain principles to which numerous facts of distribution conform, and in doing this he has performed a notable service to this field of scientific inquiry. His doctrine of Age and Area is an attempt to explain the relationships he has established, and it is of course possible that these relationships may be interpreted in some other way. I believe, moreover, that the theory of Age and Area contains a large element of truth, although I am equally convinced that the relations discovered by Dr. Willis are not nearly so damaging to the theory of natural selection as the author imagines. Although Dr. Willis reminds us that "very strong evidence, and evidence based upon definite facts, not upon *a priori* reasoning, is now required to show that the hypothesis of Age and Area is unsound," I am nevertheless impelled to give expression to some doubts in regard to the general validity of the Age and Area theory. It is with some hesitation that I venture to discuss the conclusions of a worker who has devoted years of study to a field in which I have made no original investigations, but an endeavor to understand Dr. Willis's theory and to think out its logical implications has suggested several inherent difficulties of this interesting speculation. I could not help asking myself if it were, in the nature of things, possible for nearly all small area species to be young and expanding, for this would naturally mean that species come into existence very much more rapidly than they disappear. Doubtless there has been a slow increase in the number of species of plants and animals throughout geological time, but the lifetime of a species is in most cases much less than the duration of a geological period. A few genera last through several periods, but they are quite exceptional, and long-lived species are still more exceptional. If we take a date in geological history, say the beginning of the Miocene, it is evident that most species that originated up to that time are now gone. If we may judge from the past history of life on this globe, we must conclude that at some future time as remote as the present is from the Miocene, most of our present species will be extinct and replaced by new forms. There is no gainsaying the fact that with the exception of species now living on the earth (and these are a very small fraction of the total number of species existing at some time) all the species that have arisen have also died out. Age and Area, as conceived by Willis, requires a world which is in process of being stocked with new species, and not one in which old species go out about as fast as new ones come in. If species die, and dwindle before they die, a good many small species must be relics. But this conclusion Dr. Willis refuses to admit. Of course some Cuvierian cataclysm might suddenly wipe out a whole fauna and flora, but this is not the usual process of extinction. There are records of many species that have become extinct, usually through the agency of man, and in almost all cases rarity precedes extinction, although the disappearance of the species may be more rapid than its initial spread. I do not think we know enough about the extinction of species under natural conditions which have not been altered by the meddling of man to be able to say whether the contraction of range which precedes the disappearance of a species is in general more or less rapid than its previous expansion. In any region there are a few wide-ranging and possibly old species, more of narrow range which are perhaps younger, and still more of smaller area; but why should we assume that the small species are spreading? Why may they not be both young and contracting? Not many, we may concede, are the remnants of previous wide-spread forms, but quite a few may be old species which have never been widely spread, the occupants of some peculiar ecological niche to which they are especially adapted. I can not help thinking that Dr. Willis has unduly minimized the rôle of extinction and has gotten himself into a logically untenable position, although it is one from which he may retreat without entirely abandoning his fundamental principle. Most "wides" may be old, and a large proportion of small area species may be young, but it does not follow that nearly all are marching steadily on toward a larger place in the sun.

I have looked through many of Dr. Willis's writings to find if the foregoing rather simple considerations that have troubled me have also troubled him, but I can find no adequate discussion of the situation. On reading his paper on the Endemic Flora of Ceylon,[2] one might infer that Willis fully considered the situation I have presented. In discussing a curve illustrating the origin, spread and extinction of species he says:

> Ultimately each species will reach a maximum height in the curve. It may stay there a long time, or may go up and down with the appearance on the scene of new factors affecting it. But as a good many of the newer species which come into being and climb the curve will tend to be a little better adapted than those that preceded them, we may take for granted that in the great

[2]Phil. Trans. Roy Soc. London. B. 206, p. 307. 1915.

majority of cases the species, however high it may have climbed, will ultimately begin to descend.

This is eminently sensible. On the next page, however, there occurs a footnote to the effect that "in a subsequent paper it will be shown that there is little evidence that any species are dying out." This note appears to have been added in a sort of afterthought, as if he had repented him of what he had said and concluded that he had conceded too much. I do not know what the subsequent paper is to which Dr. Willis alludes, but in an article on "The evolution of species in Ceylon, with reference to the dying out of species," published in January of the following year (1916),[3] it is stated quite definitely that "species, or at least the majority of them, do not appear to die out except by accident," and that "there is no evidence whatever that any of the angiospermous species of the Ceylon flora are dying out, and from analogy we may imagine this to be generally true." In a somewhat later paper[4] he says:

> The figures given in my various papers on this subject afford no evidence to show that any species are actually dying out. Many people at once jump to the conclusion that by this I mean that *no* species are dying out, but this is by no means the case. What the figures show is that such cases are too few to be seen in them in an unmistakable way.

These extracts and the later ones previously quoted seem to indicate that Dr. Willis has developed an increasing reluctance to admitting that species normally die out, although he rather grudgingly concedes that they may do so on rare occasions. As he has engaged in more or less controversy as to whether small area species are youngsters or relics, possibly this reluctance is one of the psychological effects of opposition, a sort of defense reaction which he has adopted in the course of supporting his argument. I confess that I can not see the logic of his position, and am led, therefore, to seek for psychological reasons for understanding why he has adopted it. Surely Dr. Willis does not expect species to last indefinitely. Does he seriously think that we are living in a geologically unique period in which species are being born many times as fast as they die? Does he believe that species are usually "killed out" by some sudden catastrophe? Or has he simply been led, through his opposition to the notion that small area species are relics, into defending an extreme position that is inherently inconsistent?

There is also another consideration that troubles me, although I admit that it is largely *a priori*. Suppose we have several species extending their range. Must not this extension be generally at the expense of some other occupants of the territory whose range becomes correspondingly restricted? The plant and animal life of any region is precariously near the saturation point, and it is absurd to suppose that species in it can expand and expand according to Age and Area without causing some other unfortunate species of the region to retire. One naturally thinks in this connection of the classical examples of the European cockroach being driven out by its Asiatic relative, and the native Australian honey bee retreating before the successful invasion of the common hive bee. With closely allied species (and it is to such that the Age and Area principle is supposed especially to apply) there is commonly acute rivalry, and the spread of one species naturally involves the retreat of another. It seems fairly evident to my *a priori* point of view that, under usual conditions, expansion and being squeezed into smaller limits are correlative phenomena, and that the two processes go on at approximately the same rate.

Sometimes, it is true, species overlay and intermingle; but in so far as closely allied forms obey Jordan's law, and they do so quite generally among the higher vertebrates and presumably also in many other groups less closely studied, they seem to constitute mutually exclusive aggregates. In any case, even when expansion goes along with interpenetration, there is antagonism and a tendency of one species to squeeze out the other. The doctrine that most small area species are relics of previously widespread forms is probably not tenable, but there is nothing in Dr. Willis's statistical data to preclude our regarding many of them as relatively young species which are gradually succumbing to pressure. This is, I believe, a very important point, especially in relation to the objections Willis has raised in regard to the efficacy of natural selection. When an attempt to make what Professor Tyndall calls the scientific use of the imagination in order to see where Dr. Willis's theory of species forming takes us, we find that we are led to a *reductio ad absurdum*. The theory at least requires modifications to bring it into harmony with the facts of extinction and the shrinkage of area which precedes extinction. When these modifications have been made I suspect that several of Dr. Willis's criticisms of natural selection, especially so far as they are based on the assumption of a regular mechanical tendency of species to spread, will fall to the ground.

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[3] *Ann. Bot.* 30, p. 1. 1916.

[4] *L. C.* 31, p. 335, 1917.