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SOME BEGINNINGS OF SPECIFIC DIFFERENTIATION IN PLANTS¹

By Dr. M. L. FERNALD

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IN these days, when the followers of some of our youthful and consequently aggressive branches of biology actually work with but few specific entities and often spend half a life-time experimenting with the vagaries of a single one under highly artificial, if not pathological conditions, we are likely to gain a distorted conception of what a species really is. Some of my friends who have had little or no broad taxonomic background and whose interest in plants awoke in the laboratory, not out-of-doors, toss about the terms species and speciation with an assurance which the more thoughtful of taxonomists have learned to avoid. It should really be remembered,

however, that, although never capable of rigidly exact definition, the species has been for centuries the primary concept of the taxonomist. In fact, two centuries ago, the great organizer of the accumulated knowledge in the natural sciences, Linnaeus, so far glorified the species as to write: "The tyro makes systems, the expert makes species."

The taxonomist, who once was the only botanist, now welcomes among a host of young brothers that increasing body of modern biologists who think chiefly of genes; but it is sometimes a bit shocking to him to be assured by them that, by drastic chemical, physical or pathological manipulations within their restricted laboratory walls, they have produced something which might be termed a new species. Perhaps; but it seems improbable that their "creations," put

¹ Read by invitation at the joint session of Section G and the affiliated Botanical Societies, at the fifth Boston meeting, December 28, 1933.

to the test, would be able to strike out into the world and successfully to hold their own, as the great majority of real species have done for millions and millions of years, in spite of wholesale physiographic changes which have altered the contours and boundaries of the continents, the positions of the seas and the temperatures of the thin stratum in which the plant-species have to live. Some of the Jurassic and early Cretaceous fossils of *Ginkgo* are apparently indistinguishable from the living *Ginkgo biloba*; Cretaceous species of *Platanus* show, to quote Seward, "almost specific identity with existing trees"; and innumerable species of Tertiary origin are still prospering, for example, the American beech, *Fagus grandifolia*, which dominates much of eastern North America. Unlike the temporary mutations of a few helpless prisoners in the laboratory, they have faced the actual world and have withstood the relentless test of competition. There are real species for you!

Although I would not for a moment imply disrespect for the painstaking efforts of my gene-hunting associates, I confess to being so old or so old-fashioned as to have more faith in the permanency of results of the slow processes of nature than in the swift and sometimes impatient ones of man; and I can not help feeling that a large experience with plants as they occur in their natural environments is more likely to give us a true evaluation of evolution than are the closet experiments on organisms under conditions which are too often not really natural and which can hardly ever be completely so.

It is, therefore, for close observation of plants in nature that I am pleading. Not long ago the taxonomist who worked only on dried material (usually the only material he can preserve and satisfactorily store for repeated comparisons) and never saw the plants in their natural surroundings was maliciously called a "closet botanist." The type is not extinct, but it is possible that the term should be applied outside the field of taxonomy. Another group is growing up: the taxonomists who do as much field-work as herbarium-study and who, consequently, reenforce their long and arduous routine in the herbarium with intimate field-experience. It is this group, taxonomists with a knowledge of natural conditions, who, perhaps, can throw some light on the great problem of specific evolution. I am, therefore, asking you to review with me a very few of the simple responses of some common plants to natural changes of environment.

Many plants are so stable in their characters and so conservative or so dependent in their requirements that their inevitable response to change of environment is death and extinction. Of such are the majority of saprophytes, the species with mycorrhiza and the highly localized relic-species. Others, more plastic, respond by certain predictable modifications of

the vegetative habit. The sensitive fern, *Onoclea sensibilis*, although seventy to one hundred million years old (or older), still fluctuates within a limited and definite range of variation. Overfeed it or stimulate it to new growth and the chances are, as every observant field-naturalist knows, that it will change from the ordinary type with sharply differentiated sterile and fertile fronds to the forma *obtusilobata*, in which one of them becomes altered. Any experimenter, unaware of the frequency of this reaction in *Onoclea* and other dimorphic ferns, might well suppose that he had created a new species; one of the most scholarly of pioneer taxonomists, Christian Sehkuhr, knowing the plant only from a strange specimen in a European collection, so treated it. Had he known it with the intimacy of the acute field-botanist in eastern America or in eastern Asia he would have realized his error.

Some other plants have less predictable mutations. Every experienced taxonomist knows one or more unresolvable puzzles in each of many large genera, plants like the *Cerastium arvense* or the *Campanula rotundifolia* complexes, in which several characters, pubescence, presence or absence of bloom or glandularity, shape, size and texture of foliage and size and shape of floral parts, seem to align themselves into scores of somewhat recognizable combinations without the natural geographic ranges or the stability over broad areas which we demand of true species and geographic varieties. These include jordanons, microspecies, biotypes, ecotypes, states, phases, forms and other biologically significant but taxonomically minor variations. Call them biotypes, ecotypes or what you will (the historically established usage of the taxonomist calls them *formae*), but do not call them species. That would indicate a confusion of ideas and a lack of understanding of long-established terminology.

To this group of highly variable organisms belong the domestic animals and plants which have proved economically most important to man. A rigidly stable species, not capable of modification under domestication, would be of little value on the farm. The stock-breeder and the plant-breeder must have plastic types with which to work. And so it happens, as Professor Goldschmidt so clearly emphasized at Chicago, that, to quote his words, "The majority of the geneticists' work is done with domestic animals and plants or with such wild forms as have given plenty of mutations under cultivation." I have never yet been asked by a geneticist to recommend to him for experimentation a fixed and unvarying species. It is not particularly satisfactory to seek for reactions from those who can not respond.

No matter how much or how little flowering plants may vary in habit and outward aspect, one final and

conclusive character is looked for by the conservative taxonomist. (I say conservative, for I can express only that view-point. When, as just happened, I pick up the latest issue of one of our American "Florals" and see two intergrading shrubs with identical foliage and fruit maintained as distinct species, with the perfectly frank statement, "Our two species . . . may be distinguished by habit alone," I find myself unable sympathetically to represent the view-point of *all* taxonomists.) If there is no appreciable modification of flowers or fruit, and especially of the seeds, the conservative student has learned to be cautious about separating species. If the flowers, fruits or seeds are fundamentally and constantly different, the plants are considered specifically separate, even though they may be superficially quite similar. It is, to quote the figures once used by Dr. Robinson at one of these meetings, the depth and impassability of the separating channels rather than their shallow breadth which is significant.

Hypoxis of the *Amaryllidaceae* is an ancient genus, with some of its species isolated in Australia, which was cut off from connection with the other continents early in the Cretaceous, the remainder in tropical and temperate southern Asia, Africa and tropical and temperate America. Superficially the plants are almost identical, but, borrowing the formula from another sphere of thought most used by the taxonomist, we find that in *Hypoxis*, as in many another genus, it is "by their fruits ye shall know them." The geographically isolated species of *Hypoxis* have seeds which are absolutely distinctive.

With *Hypoxis* in mind, as one of the thousands of genera with impassable deep channels separating its species, let us turn to more plastic types. Among the naturally plastic species in our wild flora few are more obvious in their responses to change of habitat than some of the amphibious plants. *Sagittaria cuneata* commonly fruits on muddy shores. There the adult and fertile plant develops slender petioles and arrow-shaped blades. In the seedling condition, however, the plant simulates the more primitive species of *Sagittaria* in having broad bladeless phyllodia, and only as it matures does it send up the slender-petioled aerial leaves. Let the seedlings develop under a deep current of water, where, at the normal fruiting season, they remain irretrievably drowned; then, failing to flower and fruit, the plant may, if it can reach the surface, develop one or two aerial blades, or, if the struggle to make the surface is futile, it will form nondescript structures half way between true blades and the primitive phyllodia. Such colonies, although never fruiting, will reproduce and spread, often over considerable areas, by means of subterranean stolons. Given conditions where muddy shores are always found, the fertile first type

will prevail; given a deep current and no open muddy bank, the last type will regularly appear. They are not specifically nor even varietally distinct. Both can easily be grown from the same sowing of seed; but is it unreasonable to believe that by continuance of the isolation through countless generations these traits might be gradually intensified and eventually fixed? Man's life-time is far too short to witness such stabilization, but nature works in millions, not decades of years.

One of the commonest plants of shores and flooded meadows is the meadow parsnip, *Sium suave*. Starting growth under water in spring, its first foliage is finely dissected. As the stem elongates the leaflets become less divided and at flowering time no trace of the primary foliage is retained. Let the seeds fall into deep water, however, whence the seedlings can not emerge; the leaves will become filmy, the leaflets reduced and often pectinate. This aquatic phase, so completely unlike the terrestrial, fooled the earlier taxonomists. When it was first brought to his attention by Dr. Joseph Carson, Durand, with the moral support of Asa Gray, fell into the trap and described it as a new species, *Sium Carsonii*. Nowadays we know that seeds from a single plant will produce either extreme, according to where the seeds chance to fall.

Following this same species into another extreme habitat, the river estuary, where twice a day the fresh to brackish water covers and uncovers the flats with the movements of the tides, we find a plant of wholly different aspect, with the lateral leaflets undeveloped and the terminal leaflet greatly broadened. Although this estuary phase of *Sium suave* never fruits, it makes the gesture of flowering, and finally thickens the bases of the axillary fascicles of leaves, which, bulb-like, apparently serve for vegetative reproduction. Given a continuance of the estuary conditions through a long epoch, might not *Sium suave*, forma *fasciculatum* become as fixed as are the sterile *Polygonum viviparum*, *Saxifraga cernua* and other vegetatively propagating species of broad circumpolar range and unvarying reproduction by bulblets?

Another amphibious plant which all of you must know is the species of lake margins which has long passed as the European *Polygonum amphibium*. Whether we so treat it or whether we join Amos Eaton and his followers in calling it an American species, *Polygonum natans*, is here immaterial. The aquatic plant has close, cylindric sheaths, like cuffs, long and slender petioles and oblong, round-tipped leaf-blades. It is dominant at the margins of thousands and thousands of lakes and ponds. Years ago, the late C. Hart Wright discovered in swamps of western New York a very different plant, with broad,

horizontal collars or ruffs spreading from the summits of the sheaths and with subsessile and lance-acuminate blades. Asa Gray, to whom it was sent, at once described it as a remarkable new species, *Polygonum Hartwrightii*. Subsequent botanists by the hundred came to know this unique plant as an erect species of swamps, thickets and dryish meadows. Hardly a cedar swamp in northern Maine and the Maritime Provinces lacks it, and it might there be looked upon as a typical species. The "jolt" in this case came when a country store-keeper in a Connecticut village, the late Luman Andrews, found the common aquatic plant cast up by the waves on the dry shore and, forthwith, sending up from its axils typical branches of terrestrial *Polygonum Hartwrightii*. Subsequently, the observations of Luman Andrews have been many times corroborated, and *Polygonum Hartwrightii* as a distinct species has disappeared. If the specific criterion I at first emphasized had been applied, *Polygonum Hartwrightii* would never have been called a species. Its flowers and fruits are quite like those of the aquatic plant. On the other hand, in the thickets and swamps, which have resulted from the gradual drying out of former glacial lakes and pools, *Polygonum Hartwrightii* maintains itself. In the year 1,001,933, when these areas may have become even less subject to occasional inundation, may it not perhaps be eligible for inclusion in a list of true species?

Let me refer to one other amphibious plant, the marsh cinquefoil, *Potentilla palustris*. In early summer, when the water is high, this half-shrubby species sprawls by the river-margin or in the flooded meadow, and its glabrous, dark-green foliage colors broad areas. Later, however, when the drouth of midsummer has converted the meadow into a bed of dry tinder, something has happened to the dark-green marsh cinquefoil. New vegetative shoots have sprung up, covered with silvery-silky foliage. Just as in the stranded aquatic *Polygonum*, the new shoots with silvery foliage have sprung from individual plants of quite different aspect. I leave you to make your own deductions.

Turning from hydrophytes to one of our common xerophytes, almost every one knows the bearberry, *Arctostaphylos Uva-ursi*, which trails on arid sands or over sterile rocks of the northern half of the Northern Hemisphere. In May its really beautiful flowers expand, broadly urn-shaped and whitish, with pink lobes. At the tip of Cape Cod, in sandy pitch pine woods, a party of my students discovered one October beds of bearberry flowering profusely, but with brilliant carmine and very slender, barrel-shaped corollas. This red-flowered shrub, continuing to flower through November, would anywhere pass as a remarkable new species. But, alas, when spring

comes the identical shrubs, still holding a few lingering, slender red flowers, come out with a profusion of the ordinary urceolate white corollas of everyday bearberry! Interpret the matter as you will, it is at least suggestive that the spring-flowering *Hamamelis vernalis* of the ancient Ozark Plateau and the vernal species of *Hamamelis* of the ancient flora of eastern Asia are represented throughout the more recently available area of the northeastern states and southeastern Canada by the autumn-flowering *Hamamelis virginiana*. Given a million years of undisturbed occurrence, with now and then successful fruiting, might not *Arctostaphylos Uva-ursi*, forma *heterochroma* eventually join *Hamamelis virginiana* as a finally established autumn-flowering species?

The few cases (to which I could make hundreds of additions) thus far discussed are by the careful taxonomist treated only as phases, states or forms, not even as varieties. They are individual variations of single plants. Now we will spend a few minutes on some geographic varieties, *i.e.*, variations which in distinctive or definable areas have become so thoroughly established as to be characteristic of the region.

Whereas individual plants of *Potentilla palustris* and likewise of *Potentilla Anserina*, *Dryas integrifolia* and many other species alter their pubescence with changes of moisture-content of the soil, and numerous other plants show parallel responses with increase or decrease of soil-alkalinity or -acidity, some others have stabilized their coats of trichomes over distinctive geographic areas. Thus, to continue with the plastic genus *Potentilla*, on the dry open gravels, sands and acid rocks of the Atlantic slope, *Potentilla canadensis* is a dominant plant, characterized by closely appressed silky pubescence, so insignificant as to appear merely as a slight sheen. On the ancient uplands of the Alleghenies and the Ozarks, regions which were the Cretaceous cradles of many plants whose descendants have migrated out to the areas formerly occupied by Cretaceous and Tertiary seas and Pleistocene ice, there occurs a plant identical in habit, foliage, flowers and fruit, but shaggy with long villous pubescence. Localized in two perfectly distinctive but adjacent ancient areas *Potentilla canadensis* var. *villosissima* is presumably the progenitor of the silky eastern plant which Linnaeus happened first to call *Potentilla canadensis*. The point I wish to emphasize, however, is that these two tendencies, which in many other plants occur merely as temporary fluctuations or mutations without appreciable geographic isolation, have in this case established a geographic separation. They are, consequently, geographic varieties (subspecies of some students). Hundreds of other quite parallel cases will occur to the experienced taxonomists, in *Potentilla*, *Fragaria*, *Astragalus*, *Panicum*, *Paspalum*, *Andropogon*, *Pteri-*

dium and almost any other plastic vascular genus. The extreme splitters, those who care not or know not whether a species rests on a sound basis of fundamental differences of the reproductive structures or whether it is merely a local trend with conspicuous but comparatively unimportant differences in the abundance and length of trichomes, stultify taxonomy, it seems to me, by indiscriminately treating such very minor tendencies as species, and they often actually so dignify even the mere tendencies or fluctuations which do not have a suggestion of geographic separation.

Every ten-year-old child who has had a garden knows, if he has any power of observation, that plants neglected and allowed to struggle in dried-out or sun-baked spots will have a minimum of foliage in comparison with the bulk of flowers. He also knows that individuals which grow in moister, richer or shadier situations have an excess of foliage and a minimum of flowers. When he has made that elementary deduction he has become an experimental biologist. Nature has been carrying on the same experiments on a larger scale. On the sunny meadows of our eastern states one of the joepy-weeds, *Eupatorium maculatum*, is abundant, with its broad crimson corymb clearly overtopping the reduced upper foliage. Proceed northward to the river-valleys of northern New England or the foggy coasts of Nova Scotia, the plants will be found to have larger leaves and reduced corymbs, until finally, in Newfoundland, eastern Quebec, northern Maine and the Lake Superior region the leaves so completely overtop the corymb as to mark the var. *foliosum*.

This foliose development characterizes geographic varieties of many species in the region of *Eupatorium maculatum*, var. *foliosum*. Explain them as you will, they are definitely variations which have gradually worked out a geographic or ecological segregation. But, without reproductive differences and with an abundant series of transitions, they have not yet become species. They are, however, very clearly on the way.

In the peats and damp sands of the Atlantic coastal plain one of the neatest, though insignificant, plants is *Bartonia paniculata*, found from Louisiana to Newfoundland. Throughout the South it is a consistent plant with small straw-green flowers with sharp sepals and petals. In southern New England and on Long Island, however, it becomes a little variable and in Nova Scotia this variation has become so stabilized as to rank as var. *intermedia*. On Sable Island, separated from Nova Scotia by 100 miles of sea and standing as a last unconquered remnant of the sunken coastal plain which, Professor Douglas Johnson assures us, went under approximately a million years ago (in late Pliocene or earliest Pleisto-

cene), the species is represented only by var. *sabulonensis*; but on the mainland of Nova Scotia one can get every conceivable transition from typical *Bartonia paniculata* or from the northern var. *intermedia* to the variation which on Sable Island has become an unvarying extreme. Proceeding northward across Cape Breton, the flowers become larger and more corolloid and, finally, on Newfoundland we get everywhere the thoroughly constant and unvarying large-flowered var. *iodandra*. Considered by themselves the Newfoundland and the Sable Island plants would make consistent species, but so many transitions occur that we must admit that the million years since the foundering of the northern Coastal Plain has not sufficed to dispose of the embarrassing intergrading series.

One more case, which must be my last. *Epilobium*, as every one knows, has a silky and conspicuous coma on the seed, whence the book-name, willow herb. By the current treatments of the tribe the world-wide *Epilobium* is always generically distinguished by having the coma, while the western American *Boisduvallia* lacks it. A willow herb without a coma would not be a willow herb. Nevertheless, see what has happened! The commonest and most plastic species of North America is the wide-ranging *Epilobium glandulosum*, in some northern regions with the foliose development already noted, in some others with reduced upper foliage and change of leaf-outline. The varieties are very numerous, but they all have identical seeds, with smoothish deep-brown surfaces and long white coma.

If you go to the great tidal flats of the St. Lawrence you will see the finest development of estuary imaginable. For miles and miles from well up-river above Quebec far down-river toward the Gulf, at every low tide much of the flat margin of the bed of the St. Lawrence is exposed as a seemingly endless mud-flat, freely dotted with stranded fish-weirs. Twice a day, at the rapid rise of the tide, these vast mud-flats are deeply drowned by fresh to brackish water. Only a limited number of plants can stand these rapid changes, from complete submergence in water and burying in mud to alternating periods of boiling and broiling. But, singularly enough, *Epilobium*, with one of the most perfect adaptations for wind-dispersal in a dry atmosphere, has found the inundated flats and seems to like them. The plant of the drowned estuary in habit, foliage and flowers is inseparable from the commonest variety of *Epilobium glandulosum*. But of what use is wind-dispersal to a regularly inundated and mud-encrusted plant? Absolutely of no use. Consequently or at least (either way you view it), the estuary plant in its seeds is not an *Epilobium* at all. It is unique in the vast cosmopolitan genus in having no coma whatever, and

it has further departed, not only from the terrestrial *Epilobium glandulosum*, which it superficially closely simulates, but from all other species in eastern America by altering its seeds, so that, instead of being brown and only minutely pebbled, they are gray and covered with ridges of coarse papillae. Here, at last, nature has evolved a species, *Epilobium ecomosum*.

From a purely academic view-point it would be possible to argue that *Epilobium ecomosum* is the only surviving remnant of an ancient series of sub-aquatic plants which, taking to the land, have, all over the world, evolved the coma as an adaptation for wind-dispersal. But, compared with the great geological age of the habitats of some typical *Epilobia*, that of the estuary of the St. Lawrence, available only since at least the first Pleistocene invasion, is comparatively modern. Furthermore, did time permit, I should like to discuss from the same estuary of the St. Lawrence a beggar tick (*Bidens*) which has no awns, such as regularly characterize the terrestrial species of *Bidens* and supply the generic name. Of what use would awns be in such a habitat? On land

they indiscriminately seize hold of the fur or the coats of every passing animal, but the fish of the lower St. Lawrence are too smooth to function as dispersal-agents, even for *Bidens*.

We may reason that in these and several other similar cases, one of the numerous predetermined variations of *Epilobium* or of *Bidens* or of some other genus fortuitously sprang into being in the estuary of the St. Lawrence and in this satisfactory environment has found opportunity to prosper, or we may prefer to view the peculiar environment itself, as so often seems to be the case, as molding an old species into something more fitted to the special surroundings. Whichever interpretation we choose, the simple fact remains that the field-botanist who would look successfully for thoroughly differentiated local species and pronounced geographic varieties (incipient species) has learned (as Charles Darwin did before him) to go to restricted areas which for ages have been ecologically or physiographically unique or which for at least a thousand millenniums have had remote or insular or peninsular isolation.

DEVELOPMENT OF OUR EARLY KNOWLEDGE CONCERNING MAGNIFICATION

By Professor WILLIAM W. FORD

THE JOHNS HOPKINS UNIVERSITY

ANY clear transparent object with one convex surface and one flat surface or two convex surfaces acts as a magnifier, and the statement is often made that the use of such materials for magnification goes back many centuries. Thus large convex pieces of rock crystal were found by Layard in the ruins of a palace at Nimrud below the ancient city of Nineveh in Assyria. It is now agreed that such pieces of crystal could not have been used as lenses to enlarge the size of objects because of their uneven surfaces and bands, but that they probably served as ornaments to be worn on the chest. Various references to spectacles can be found in ancient Chinese writings, but such glasses were undoubtedly employed for the protection of the eyes and not as an aid to vision. A knowledge of the principle of magnification may be very old, however. Euclid in the third century B.C. investigated the laws of refraction, and Seneca apparently grasped the idea. In his "Questiones Naturales," written about 63 B.C., he states that "letters, however small and dim, are comparatively larger and distinct when seen through a glass globe filled with water." The appreciation of this principle is also closely associated with the manufacture of spectacles with the

distinct purpose of improving the sight. These probably arose among the Venetian glass workers, and their discovery is usually attributed to Salvino d'Amato degli Amarti of Florence and Allesandro della Spina of Pisa. The evidence for this is not entirely satisfactory. Cole¹ says that Francesco Redi (1626-1697), physician, naturalist, poet, mentions probably the first written reference to spectacles in a manuscript, dated 1289, written by a monk who says that he could neither read nor write without the glasses called *occhiali* for the improvement of his vision. Rolleston,² however, says that the "Lilium Medicinæ" of Bernard de Gordon of Montpellier, published in 1305 or 1306, contains the first notice of spectacles.

How far back in history the use of simple lenses goes is equally doubtful. It has sometimes been claimed that ancient gems could not have been cut and fashioned into jewelry without an aid to the sight, and that engraved and illuminated texts required some magnification for their preparation.

¹ Cole, Ann. Med. Hist., viii: 4, 347-359, 1926.

² Rolleston, "Internal Medicine in Clio Medica," p. 35, 1930.