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THE ORIGIN OF SPECIES THROUGH ISOLATION.

For me, it is the chorology of organisms, that is to say, the study of all the important phenomena embraced in the geography of animals and plants, which is the surest guide to the study of the real phases in the process of the formation of species. (Moritz Wagner.)

It is now nearly forty years since Moritz Wagner (1868) first made it clear that geographical isolation (räumliche Sonderung) was a factor or condition in the formation of every species, race or tribe of animal or plant we know on the face of the earth. This conclusion is accepted as almost self-evident by every competent student of species or of the geographical distribution of species. But to those who approach the subject of evolution from some other side the principles set forth by Wagner seem less clear. They have never been confuted, scarcely even attacked, so far as the present writer remembers, but in the literature of evolution of the present day they have been almost universally ignored. Nowadays much of our discussion turns on the question of whether or not minute favorable variations would enable their possessors little by little to gain on the parent stock, so that a new species would be established side by side with the old, or on whether a wide fluctuation or mutation would give rise to a new species which would hold its own in competition with its parent. In theory, either of these conditions might exist. In fact, both of them are virtually unknown. In nature a closely related distinct species is not often

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quite side by side with the old. It is simply next to it, geographically or geologically speaking, and the degree of distinction almost always bears a relation to the importance or the permanence of the barrier separating the supposed new stock from the parent stock.

A flood of light may be thrown on the theoretical problem of the origin of species by the study of the probable origin of species with which we may be familiar, or of which the actual history or the actual ramifications may in some degree be traced.

In such cases, one of the first questions naturally asked is this: Where did the species come from? Migration forms a large part of the history of any species or group of forms. The fauna of any given region is made up of the various species of animals living naturally within its borders. The flora of a region is made up of the plants which grow naturally within its borders. Of all these, animals and plants, the inhabitants of most regions are apparently largely migrants from some other region. Some of them have entered the region in question before acquiring their present specific characters; others come after having done so. Which of these conditions apply to any individual case can generally be ascertained by the comparison of individuals along the supposed route of migration. Thus the Tahoe trout is clearly a migrant from the Columbia River, its separation apparently dating from the time when the former lake basin of Nevada (Lake Lahontan) found its drainage in the Columbia. We know that the present specific characters of this trout were assumed within its present range, because these traits are not found in any other trout along the supposed line of its migrations. On the other hand, we feel certain that the salmon of New England originated as a species in Europe. In extending its range from its primitive home, it has not undergone any

material change or acquired any distinctive characters, while both in Europe and in America it has more or less modified landlocked variants.

The region from which a group of animals is supposed to be derived is spoken of as its center of dispersion.

Thus the various forms of trout, originally of marine origin, seem to have diverged from the Siberian region, eastward and westward. This region is, therefore, the center of dispersion of trout. In like manner the tanagers have their center of dispersion in South America; the humming birds also. The lemurs have their center of dispersion in Madagascar, and the cat tribe in tropical Africa.

In general, although not always, the original home of any group of animals will show more varied forms than those in any other region. There may be some representatives more highly specialized, more primitive forms are likely to be preserved, more degenerate forms may be developed, and if the type is represented by fossils, these also may exhibit a larger range of forms and characters than will be found in regions occupied through later migrations.

It is evident that the nature of any fauna bears an immediate relation to the barriers, geographical or climatic, that surround it. Whenever the free movement of a species is possible, this involving the free interbreeding of its members, the characters of a species remain substantially uniform.

Whenever free movement and interbreeding is checked, the character of the species itself is altered. This is the meaning of Coues's pregnant phrase: 'Migration holds species true; localization lets them slip.' In other words, free interbreeding swamps the incipient lines of variation, and this in almost every case. On the other hand, a barrier of any sort brings a certain group of individuals together. These are subjected to a selection different from that

which obtains with the species at large, and under these conditions new forms are developed. This takes place rapidly when the conditions of life are greatly changed so that a new set of demands are made on the species, and those not meeting them are at once destroyed. The process is a slow one, for the most part, when the barrier in question interrupts the flow of life without materially changing its conditions. But this is practically a universal rule: A barrier which prevents the intermingling of members of a species will with time alter the relative characters of the groups of individuals thus separated. These groups of individuals are incipient species and each may become in time an entirely distinct species if the barrier is really insurmountable.

In regions broken by few barriers, migration and interbreeding being allowed, we find widely distributed species, homogeneous in their character, the members showing individual fluctuation and climatic effects, but remaining uniform in most regards, all representatives slowly changing together in the process of adaptation by natural selection. In regions broken by barriers which isolate groups of individuals we find a great number of related species, though in most cases the same region contains a smaller number of genera or families. In other words, new species will be formed conditioned on isolation, though these same barriers may shut out altogether forms of life which would invade the open district.

Thus throughout the eastern United States, unbroken by important barriers, there is but one true species of chipmunk, *Tamias striatus*, and one species of shore-lark (*Eremophila alpestris*). In California, broken by many barriers of various sorts, there are a dozen or more different kinds of chipmunks, species and subspecies. But in the eastern states the fauna at large

is much greater, because many types of birds and other animals have found entrance there, forms which are excluded from California by the barriers which surround that region.

In the great water basin of the Mississippi many families of fishes occur and very many species are diffused throughout almost the whole area, occurring in all suitable waters. Once admitted to the water basin, each one ranges widely and each tributary brook has many species. In the streams of California, small and isolated, the number of genera or families is much smaller. Each species, unless running to the sea, has a narrow range, and closely related species are not found in the same river.

The fact last mentioned has a very broad application and may be raised to the dignity of a general law of distribution.

Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort.

The nearest relative of the Tahoe trout (*Salmo henshawi*) is the cut-throat trout (*Salmo clarki*), its parent form, which is found in the Columbia and Missouri, the two rivers interlacing at their fountain heads. The nearest relatives of the cut-throat are two forms apparently descended from it, *Salmo virginalis*, of the basin of Utah, and *Salmo stomias*, of the Platte. Next to the latter is *Salmo spilurus*, of Rio Grande, and then *Salmo pleuriticus*, of the Colorado. The latter in turn may be the parent of the Twin Lakes trout, *Salmo macdonaldi*. Always the form next away from the parent stock is onward in space across the barrier.

The nearest relative to almost any Hawaiian species of fish is found in Polynesia; that to any Polynesian species is

found on the East Indies. From the East Indies we find lines diverging to the Red Sea, to the Cape of Good Hope, to Japan, to Polynesia and Hawaii, to Australia and New Zealand. We, therefore, consider the East Indies the center of dispersion or primitive home for most types of tropical fishes. At the Isthmus of Panama the nearest relative of many species of fishes is found across the isthmus, in the West Indies. Thus the red snapper of Panama, *Lutianus colorado*, finds its analogue in the red snapper of the Caribbean Sea—*Lutianus aya*. The large black snapper of Panama, *Lutianus novemfasciatus*, finds its nearest relative in the Cubera of the Caribbean, *Lutianus cyanopterus*. The same is true of perhaps 300 other species at Panama, enough to show that the resemblance across the isthmus is not a matter of accident. The divergence between these separated forms dates apparently from the time, in the late Miocene, when the seas ceased to flow together across this isthmus.

Again, in the Atlantic, the nearest relative of the Allice shad of the north of Europe (*Alosa finta*) is the Thwaite shad (*Alosa rufa*) of farther south. Another near relative is the American shad (*Alosa sapidissima*) of our Atlantic coast. This again finds its nearest ally in the Gulf shad (*Alosa alabamæ*), and this once more in the Ohio shad (*Alosa ohioensis*).

Always the species nearest alike in structure are not found together, nor yet far apart, and always a barrier lies between. Where two closely allied forms are not found to intergrade they are called distinct species. If we find actual intergradation, the occurrence of specimens intermediate in structure, the term subspecies is used for each of the recognizable groups, thus connected.

Thus of the bluebird, *Sialia*, we have in America three main forms, the one boreal,

found in northern and western mountain regions, blue above and below alike, known as *Sialia arctica*. Another form, blue above and brown below, inhabits the whole region east of the Rocky Mountains. This is *Sialia sialis*, the common bluebird of the east, 'with the sky on its back and the earth on its breast.' In the warmer parts of the mountain region, Texas to California and southward, is still another blue bird, much like the second, but darker in color and with a large patch of brown on the back as well as on the breast. This is *Sialia mexicana*. These three are considered as distinct species because there is no evidence that intergradations occur in any part of their range. One of these species, *Sialia mexicana*, has been split up into subspecies, and this is related to the fact that its range is crossed by barriers greater than those which check the movement of the others. The typical *Sialia mexicana* is found in Mexico. *Sialia mexicana bairdi* represents it in the Rocky Mountain region, and *Sialia mexicana occidentalis*, in the Pacific Coast states. A local form, *Sialia mexicana anabelæ*, is found on the mountain called San Pedro Martir, in Southern California. Along the border line between *Sialia sialis* and *Sialia mexicana*, in Arizona and Mexico, the eastern bluebird throws off shoots called *Sialia sialis azurea*.

Widely distributed across the United States and from southern Canada to Arizona, we have the yellow warbler, *Dendroica æstiva*. This bird is chiefly yellow, olive on the back with chestnut streaks on the sides, tail feathers colored like the body, and without the white spot on the outer feathers shown in most of the other types of wood warblers composing the genus *Dendroica*.

The yellow warbler throughout its range is very uniform in size and color. Its nearest relative differs in having a shade

less olive on the back and the brown streaks on the sides narrower. This form is found in the Sonoran region, and, as along the Rio Grande, it intergrades with the first; it is called a subspecies, *Dendroica aestiva sonorana*. Further south, in central Mexico, this form runs larger in size and is recorded as *Dendroica aestiva dugesi*. Northward, through to Alaska, we have an ally of the parent bird, but smaller and still more greenish. This is *Dendroica aestiva rubiginosa*.

In the West Indies the golden warblers migrate not from south to north, but from the shore to the mountains, and possibly in consequence of the less demand of flight, the wing is shorter and more rounded, while the tail is longer. As these forms do not clearly intergrade with those of the mainland, and, for the most part, not with each other, they are held to represent a number of distinct species, although doubtless derived from the parent stock of *Dendroica aestiva*. Some of these West Indian forms are relatively large, the wing more than five inches long, and the longest known of these, the type of the species for this reason, found in Jamaica, is called *Dendroica petechia*. On the island of Grand Cayman is a similar bird, a little smaller, *Dendroica auricapilla*. Of a deeper yellow than *petechia*, and equally large, is the golden warbler of the Lesser Antilles ranging from island to island, from Porto Rico to Antigua. This form, first known from St. Bartholomew, is *Dendroica petechia bartholemica*. A smaller bird, a little different in color, takes its place in the Bahamas. This is *Dendroica petechia flaviceps*.

In Cuba the golden warbler is darker and more olive, with other minor differences from the form called *bartholemica*, of which it may be the parent. This is *Dendroica petechia gundlachi*. A similar bird, but with the crown distinctly chestnut, is *Dendroica petechia aureola*, the

golden warbler of the Galapagos and Cocos Islands, off the coast of Ecuador and Peru. Scattered over other islands are smaller golden warblers with the wing less than five inches long, and with the crown tawny red, as in *aureola*. These are known collectively as *Dendroica ruficapilla*, the type being from Guadeloupe and Dominica. More heavily streaked, with the crown darker in color, is the golden warbler of Cozumel, *Dendroica ruficapilla flavivertex*, and with very similar but with darker crown is *Dendroica ruficapilla flavida*, of the island of St. Andrews. Always the nearest form lies across the barrier, and among these forms the chief barrier is the sea. With a darker chestnut crown is *Dendroica ruficapilla rufopileata*, of the island of Curaçao, and still darker bay is the crown of *Dendroica ruficapilla capitalis*, the golden warbler of the Barbadoes.

Still other golden warblers exist, with the chin and throat chestnut as well as the crown. One of these, olive green on the back, is *Dendroica rufigula*, of Martinique. The others are more yellow. One of these, with the sides heavily streaked, inhabits the isthmus region, *Dendroica erythachoides*, called a distinct species, because no intergradations have been made out. Another more faintly streaked replaces it on the Atlantic coast from Yucatan to Costa Rica, *Dendroica bryanti*, while the Pacific coast, from Sinaloa to Costa Rica, has another form, with still fainter markings, *Dendroica bryanti castaniceps*. An extreme of this form with the throat and breast tawny, but not the crown, is found in Jamaica again and is known as *Dendroica eoa*. In this case, which is one typical of most groups of small birds, the relation of the species to the barriers of geography is so plain as to admit of no doubt or question. Given the facts of individual fluctuation and of heredity, it is manifest that while natural selection may

produce and enforce adaptation to conditions of life, the traits which distinguish species bear little relation to utility. The individuals which, separated from the main flock, people an island, give their actual traits to their actual descendants, and the traits enforced by natural selection differ from island to island. If external conditions were alike in all the islands the progress of evolution would perhaps run parallel in all of them, and the only differences which would persist would be derived from differences in the parent stock. As some difference in environment exists, there is a corresponding difference in the species as a result of adaptation. If great differences in conditions exist, the change in the species may be greater, more rapidly accomplished, and the characters observed will bear a closer relation to the principle of utility.

Doubtless wide fluctuations or mutations in every species are more common than we suppose. With free access to the mass of the species, these are lost through interbreeding. Isolate them as in a garden or an enclosure or on an island, and these may be continued and intensified to form new species or races. Any horticulturist will illustrate this.

At the risk of becoming tedious we must continue these illustrations. The contention is not that species are occasionally associated with physical barriers, which determine their range, and which have been factors in their formation. It may be claimed that such conditions are virtually universal. When the geographical origin of a species can not be shown it is because the species has not been critically studied, from absence of material or from absence of interest on the part of naturalists, this showing itself often in a semi-contemptuous attitude of morphologists and physiologists towards species mongers and towards outdoor students of nature generally. In a few cases, a species ranges widely over the

earth, showing little change in varying conditions and little susceptibility to the results of isolation. In other cases, there is some possibility that saltations, or suddenly appearing characters, may give rise to a new species within the territory already occupied by the parent form. But these cases are so rare that in ornithology, mammalogy, herpetology, conchology and entomology, they are treated as negligible quantities. In the distribution of fishes the same rules hold good, but as the material for study is relatively far less extensive and less perfectly preserved than with birds and insects, we have correspondingly less certainty as to the actual traits of species and subspecies, and the actual relation of these to the intervening barriers.

The American genus *Zonotrichia* comprises the group of streaked finches known as white crowned sparrows. Most of these agree in their grayish brown coloration, streaked with darker brown, with two black stripes on the crown of the head, the wings with two white bars and tail without white feathers. The wings and tail are long, the bill small, and there is little else to separate them from the great body of streaked sparrows, amidst which the white-crowned stand as among the largest in size.

In most of the group the crown of the head is whitish between the two black stripes. In one group of these there is no yellow on the head, these being the typical white crown sparrows, *Zonotrichia leucophrys*. The common form breeds in the Rocky Mountain region and northeastward to Labrador. It has a black patch or stripe before the eye. Northwestward, from Montana to Alaska, these sparrows have the space before the eye whitish. These are *Zonotrichia leucophrys gambeli*. Southward, coastwise, from Vancouver Island to Monterey, California, the edge of the wing becomes yellow and we have *Zonotrichia leucophrys nuttalli*.

East of the Rocky Mountains, in the same region as the typical *leucophrys*, we have the white-throated sparrow, with yellow in front of the eye, and some other differences. This is *Zonotrichia albicollis*. It does not cross the mountains and no subspecies are recognized, unless indeed the species *Zonotrichia leucophrys* be one of the offshoots. Two other species, distinct so far as we know, are recognized, *Zonotrichia coronata*, the golden crowned sparrow, breeding in Alaska, and the stately Harris sparrow, *Zonotrichia querula*, of the interior plains, migrating from Missouri and Minnesota to the Saskatchewan region. In this species the top of the head is black, with stripes of either white or yellow.

Besides these differences of color, each species has some slight peculiarity of form. *Zonotrichia albicollis*, for example, having a rounded wing and *Zonotrichia coronata* a longer tarsus than the other species.

In a discussion of the origin of certain species of chickadee Joseph Grinnell¹ makes the following observations:

It is *isolation*, either by barriers or by sufficient distance to more than counterbalance inheritance from the opposite type that seems to me to be the absolutely essential condition for the differentiation of two species, at least in birds. A strong argument in support of this conviction is that we never find two 'subspecies' breeding in the same faunal area, and no two closely similar species, except as can be plainly accounted for by the invasion of one of them from a separate center of differentiation in an adjacent faunal area (example, *Parus rufescens* of the West Coast fauna, and *Parus gambeli* of the arid Sierras meet in the Siskiyou mountains). * * *

The extremest intra-competition does not ensue until after further discrimination is impossible. * * *

Two species of approximately the same food habits are not likely to remain long evenly balanced in the same region. One will crowd out the other: the one longest exposed to local conditions and hence best fitted though ever so slightly will sur-

vive to the exclusion of any less favored invader. However, should some new contingency arise, placing the native species at a disadvantage, such as the introduction of new plants, then there might be a fair chance for a neighboring species to gain a foothold, even ultimately crowding out the native form. For example, several pairs of the Santa Cruz chickadee (*Parus rufescens barlowi*) have taken up their abode in the coniferous portion of the arboretum at Stanford University, while the plain titmouse prevails in the live oaks of the surrounding valley.

* * * The greatest rate of reproduction is presumably where the species finds itself best adapted to its environment, and this is also where the death rate is least, unless an enemy rapidly multiplies so as to become a serious check. * * * In wide ranging species subcenters arise. * * * From each of these new centers of distribution, there will be a yearly radiating flow of individuals into the adjacent country so as to escape intra-competition at any one point.

Not long since the writer addressed to certain leading ornithologists of the United States a circular letter, as given below. Certain typical answers to this letter are appended, all agreeing in general with the proposition stated above.

In considering the proposition that species in general arise in connection with geographic or topographic isolation, will you kindly answer briefly the following questions?

1. Do two or more well founded subspecies ever inhabit [breed in] the same region? If so, give examples.
2. If so, how do you explain the fact?
3. Would you regard a form as a 'subspecies' if coextensive in range with the species with which it intergrades?
4. Are there cases where two species inhabiting exactly the same region are closely related, and more closely than any other species is in either one? If so, give examples.

LEONARD STEJNEGER.

Before answering the four questions contained in your letter of February 21, just received, allow me to make a few general remarks.

I suppose that by inhabit you mean propagate, since many migrating subspecies spend part of their time in the territory of the other subspecies. It may probably be necessary to further qualify the word *propagate* by adding *simultaneously*,

¹ *Auk*, July, 1904, p. 372.

since it is thinkable at least that the subspecies might have become 'isolated' in the same locality by adopting different times of propagating. Might not such cases occur among fishes? I have also a sort of suspicion that it may occur, or may have occurred earlier, in some migratory birds on both sides of the equator. Altogether, I wish to be very reserved in my answers and I would have you understand an *obligato* 'so far as I know' added to all of them. The fact is, that the records when it comes to distinguish between the propagation habitat and the general habitat of the species are so defective that no fully reliable conclusions can be drawn from them.

1 and 2. I know of no well-founded subspecies propagating simultaneously in the same locality (I would avoid the word region as not restricted enough).

As a matter of fact I can not well conceive of two subspecies propagating simultaneously in the same locality except perhaps during a short time under the following supposition as shown by an example:

Suppose the so-called *Lanius major* of Siberia and *Lanius excubitor* were only subspecifically distinct, *i. e.*, that they had not yet developed beyond a certain degree of character stability along the original territorial line separating them somewhere in Central Asia (a supposition I do not admit, though I do not deny the possibility, the data at hand being inconclusive). Now suppose both species extended their range westward, *L. excubitor* to central Europe thence north to the Scandinavian peninsula *viâ* Denmark, while *L. major* pushed northwestward over Finland to northern Norway (and these suppositions I believe are correct!). Suppose further that the breeding ranges of both subspecies met and finally overlapped, say in some localities in Finmarken (and there are indications that they do, though the records are anything but satisfactory). The chances are, of course, that in these localities the two subspecies would mix, but for some time at least it is probable that a certain percentage of both might continue to breed pure alongside of each other. Though all this is mere speculation it is probably legitimate to carry the supposition a step further. Finmarken is the most extreme end of the range of both (supposed) subspecies, it is then not unnatural to conclude that in the specimens meeting there the characters might have become so fixed that the two forms would react on each other as two distinct species, though at their original dividing line they might

still remain in the imperfectly differentiated stage.

3. No, as a rule not. But *if* as I hinted above the isolation were one of time of spawning, for instance, concomitant with which a certain amount of structural differentiation had taken place, then I can conceive of such a state as indicated in question 3, *viz.*, that the ranges (in space) of both subspecies might be coextensive.

4. There are a few cases where *apparently* two species inhabiting exactly the same region (these terms restricted as above), are *apparently* more closely interrelated than to any other. As an example I may quote two Japanese birds, *Cettia cantans* and *C. cantillans*, the chief and possibly the only difference being the constantly greater size of the former. Yet we are told that they occur in exactly the same localities. I used the word *apparently* above because in the first place the *exact* relationship of the two species is not ascertained, and in the second, the records of the breeding ranges of both are not as complete as might be desired. That the two forms are distinct and do not intergrade seems certain. Altogether I do not pretend to understand the case.

There are a few other similarly puzzling cases, for instance, that of *Phylloperne borealis* and the so-called subspecies *xanthodyas* but apart from the fact that in this case the latter is not coextensive with the former only occupying part of the territory, the records are so incomplete and defective the chances are the puzzle may be easily solved when all the facts are known.

The case of various forms for crossbills might also be cited. In their case it almost looks as if each band is kept isolated by their gipsy-like habits, though it is just possible that they may have evolved different breeding periods or different food making them dependent on the latter for the selection of their temporary breeding locality. At any rate, the isolation does not seem to be geographical or topographical.

I hope I have been able to make my standpoint clear, *viz.*, that two geographical subspecies can not propagate in the same locality (except in rare cases illustrated by the *Lanius* example), but that there are other kinds of isolation—or possibly better: segregation, which—though more rarely—may produce subspecies—eventually species when the incomplete differentiation has become complete,—capable of living side by side in the same locality.

WILLIAM BREWSTER.

I have no knowledge based on personal experience that two well-marked subspecies of the same

species of bird ever *breed* in the same region. It is, of course, by no means unusual for two forms subspecifically isolated to occur together during migration or in their winter homes.

If I understand your fourth question rightly I should say that there are a good many known cases of species more closely related to one another than to other species occurring (in breeding) in the same region. The best examples of this that occur to me are the Allen and Least flycatchers, the blue-winged and the golden-winged warblers (these two species interbreed fairly and their hybrid offspring is *fertile*), and the Swainson's and Bicknell's thrushes. All these breed in New England and the species mentioned in pairs breed to the same covers. I think that in England excellent examples may be found among the very closely isolated warblers belonging to the family Turridæ and the family Sylviinæ.

I certainly should be loath to believe that two birds which were subspecies of the same species could breed, at least in the same area.

C. HART MERRIAM.

Your letter making inquiries as to coextensive ranges of subspecies of the same species, and so on, reached me some little time ago, but owing to pressure of other matters I have not been able to reply earlier. My answer to questions 1, 2 and 3 was no, from the first. I felt a little uncertain about the fourth question, and have spent some time in running over lists of birds and mammals in order not to make a mistake. After careful consideration I must answer this question in the same way as the others, as I fail to find any two closely related species inhabiting exactly the same region.

JOSEPH GRINNELL.

In reply to your recent circular, I offer the following:

In birds several subspecies may occur in the same region in *winter*, because of their seasonal scattering. But I know of not even one case where two subspecies *breed* in precisely the same region. I have run down two alleged cases—both proved irrelevant.

My criterion for diagnosis as subspecies is—two forms connected by a continuous series of intergrades uninterruptedly covering the interlying ground. If a geographic hiatus exists (as in island races), even though intermediates may *apparently* bridge over the difference in mean characters, I call the two forms *species*. I can see no difference between species and subspecies, except an average one in *degree* of differentiation;

and that fluctuates with personal opinion (e. g., note A. O. U. rulings from year to year!). I am about ready to deny the value of trinomials in nomenclature on this account. Call all distinguishable groups of individuals *species*, as Sharpe tries to do in his 'Hand-List of Birds.' I know of no case where two species inhabiting the same region are 'closely' related, or even more closely related than any other species is to either one.

I believe in *isolation* either by barriers, or by sufficient distance to more than counterbalance invading inheritance from the opposite extreme (geographically) as being one *essential* factor in the differentiation of species.

LEVERETT MILLS LOOMIS.

1, 2. I know of no instance.

3., No.

4. I do *not* recall a case among the Tubinares, particularly in the closely related species in *Oceanodroma*, *Puffinus*, *Ætrelata*; of course 'exactly the same region' in these birds would be the breeding grounds.

CHARLES H. GILBERT.

In attempting to reply to your circular letter concerning subspecies, I am limited by the fact that well marked subspecies are hardly known in ichthyology. Unless the term shall be finally applied to such local forms as the fresh-water sticklebacks, or to the minutely variant form characteristic of different tributaries of the same hydrographic basin, I see no probability of the subdivisions of fishes beyond the species. I can not answer your questions, therefore, on the basis of personal experience with subspecies, a fact which prevents my views from having any weight. I may, however, venture the following suggestions:

The answer to all your questions will depend upon the definition given the terms 'range' and 'region.' It might well be found, for example, that two subspecies of song sparrow would occupy the Santa Clara Valley, one confined to the tule swamps, the other to the dry uplands. That two subspecies should have coextensive range and live in the same habitat within the range, would seem impossible from the accepted definition of subspecies. I refer here to the older definition of subspecies, for many well known zoologists have recently adopted the view that subspecies are determined by the small amount of divergence rather than the ascertained fact of intergradation. To those who so hold, anything would be possible with subspecies which would be possible with species.

I know of no example under question 4.

WALTER KENRICK FISHER.

1. In *Melospiza cinerea pusillula* Ridgway and *M. c. santæcrucis* Grinnell we have two conspecific races inhabiting the same region but occupying different habitats.

2. *Santæcrucis* (a distinguishable but very closely related race to *cooperi* Ridgway, of the San Diegan-Los Angeles district), dwells in the valleys and on lower mountain slopes of the Santa Cruz Mt. peninsular, and as far south as southern Monterey Co., California. It is common along the fresh-water streams emptying into both sides of the south arm of San Francisco Bay. But *M. c. pusillula* breeds only on the marshes, among the Salicornia. Its range is consequently surrounded by that of *M. c. santæcrucis*. East of Palo Alto one can stand by nests of *santæcrucis* and be within shouting distance of many nests of *pusillula*. Yet the two races never, during the breeding season, encroach upon one another's domain. The *M. c. samuelis* of Baird occupies the salt marshes along the northern arms of San Francisco Bay. So far as known it does not intergrade with *M. c. pusillula*.

3. Not if coextensive in habitat throughout a large part of the range of both forms. If intergradation was proved beyond a doubt it might be shown that one race had encroached upon another over part of its range. Intergradation has been satisfactorily established in so few cases that one would be justified in calling such forms species.

4. The only case I can recall is that of *Empidonax hammondi* and *E. wrighti*, which are practically indistinguishable out of hand. They breed commonly in the high Sierra Nevada and over western North America. So far as genetic relationship is concerned there is a probability that *hammondi* may be a descendant of the eastern *minimus* stock, while *wrighti* may be nearer *E. fulvipectus* (S. Mexico).

I have written out the only cases I know of which will bear on your questions. The song sparrow case is easily explained by a difference of habitat. The word 'region' is of course susceptible to many interpretations. In California where zones are wonderfully juxtaposed in a sort of nature's crazy-quilt one has to be unusually specific as to locality. Birds labeled Santa Clara Valley, for instance, would considerably mislead one unacquainted with the region, if he happened to receive specimens of two subspecies of song sparrow.

Referring to the land snails of the island of Oahu (Hawaii), Alfred Russel Wallace quotes from Rev. J. T. Gulick the statement that the island has in its wooded portions about 175 species of land-shells represented by 700 or 800 varieties.

We frequently find a genus represented in several successive valleys by allied species, sometimes feeding on the same, sometimes on allied plants. In every case the valleys that are nearest to each other furnish the most nearly allied forms, and a full set of the varieties of each species presents a minute gradation of forms between the more divergent types found in the more widely separated localities.

Similar conditions are recorded among the land snails in Cuba and in other regions. In fact, on a smaller scale, the development of species of land and river mollusks has everywhere progressed on similar lines with that of birds and fishes. Many other illustrations of the same sort, drawn from almost all groups of animals, have been given by Dr. Moritz Wagner, whose epoch-making work has not received from writers on organic evolution the attention it deserves. Perhaps one cause of this neglect is found in Wagner's persistent opposition to the theory of natural selection and his insistence on isolation and migration as virtually the only factors in species forming. But to recognize isolation as practically a necessary condition in the subdivision of species need not necessarily eliminate or belittle any other factor. Isolation is a condition, not a force. Of itself, it can do nothing. Species change or diverge with space and with time; with space, because geographical extension divides the stock and brings new conditions to part of it; with time, because time brings always new events and changes in all environment.

One of the most remarkable cases of group evolution is that of the song birds of Hawaii, constituting the family of Drepanidæ. In this family are about forty species of birds, all much alike as to

general structure, but diverging amazingly from each other in the form of the bill, with, also, striking differences in form of body and in plumage. In almost all other families of birds the form of bill is very uniform within the group. It is correlated with the feeding habits of the bird, and these in all groups of wide range become nearly uniform within the limits of the family. With a great range of competition, each type of bird is forced to adapt itself to the special line of life for which it is best fitted. But with many diverging possibilities and no competition, except among themselves, the conditions are changed, and we find Drepanidæ in Hawaii fitted to almost every kind of life for which a song bird in the tropics may possibly become adapted.

In spite of the large differences to be noted, there can be little doubt, as Dr. Hans Gadow, Mr. H. W. Henshaw and others have shown, of the common origin of the Drepanidæ. A strong peculiar goat-like odor exhaled in life by all of them affords one piece of evidence pointing in this direction. There is, moreover, not much doubt that the whole group is descended from some stock belonging to the family of honey-creepers, Cœrebidæ, of the forest of Central America. Each of the Hawaiian islands has its species of Drepanine birds, some olive green in color, some yellow, some black, some scarlet and some variegated with black, white and golden. The females in most cases, like the young, are olive green. On each island, most of the species are confined to a small district, to a single kind of thicket or a single species of tree, each species being especially fitted to these localized surroundings. With the destruction of the forests some of these species are already rare or extinct. With high specialization of the bill they lose their power of adaptation.

In each of the several recognized genera there are numerous species, mostly thus specialized and localized, relatively few species being widely distributed throughout the islands.

Most primitive of all, least specialized and most like the honey creeper ancestry, is the olive green *Oreomystis bairdi* of the most ancient Island of Kauai. This bird has a small straight bill, not unlike that of the slender-billed sparrow. It is said to be the most energetic and ubiquitous of the group, feeding on insects on the trunks of trees. If we assume that *Oreomystis*, or some other of the genera with short and slender bills, represents the original type of Drepanidæ, we have two lines of divergence, both in directions of adaptation to peculiar methods of feeding.

Next to *Oreomystis*, on the one hand we have *Loxops* and *Himatione*, with the bill pointed, a little longer than in *Oreomystis*, and slightly curved downwards. The species, red or golden, of these two genera are distributed over the islands, each on its own mountain or in its own particular forest. *Vestiaria*, another genus, remarkable for its beautiful scarlet plumage, has the bill very much longer and strongly curved downward. *Vestiaria coccinea*, the iiiiwi of the islands, lives among the crimson flowers of the ohia tree (*Metrosideros*) and the giant lobelia, where it feeds chiefly on honey, which is said to drop from its bill when shot. According to Mr. S. B. Wilson, the scarlet sickle-shaped flowers of a tall climbing plant of *Strongylodon lucidus* found in these forests 'mimic in a most perfect manner both in color and shape the bill of the iiiiwi' so that the plant is called nukuiwi (bill of the iiiiwi).

The next genus, *Drepanis*, has the sickle bill still further prolonged, forming a segment of a circle, and covering nearly 50 degrees. *Drepanis pacifica*, one of the

species, has the bill forming about one fourth of the total length. The species of this genus, black and golden in color, were very limited in range, and are now nearly or quite extinct. Still another group with sickle bills, *Hemignathus*, diverges from *Vestiaria* in having the upper mandible only very long and decurved, the lower one being relatively short, straight and stiff. The numerous species are mostly golden-yellow in color. Some or all of them use the lower mandible for tapping the trees, after the fashion of woodpeckers, while with the long and flexible upper one they reach into cavities for insects or insect larvæ or suck the honey of flowers. The group contains long-billed forms like *Hemignathus procerus* of Kauai, in which the bill is more than one fourth the total length of the bird, and short-billed forms like *Hemignathus* or *Heterorhynchus olivaceus* of Hawaii. In the short-billed forms the two mandibles are most unlike; the upper very slender, much curved and about one fourth the length of the rest of the body, the lower mandible half as long and thick and stiff. These birds feed chiefly on insects in the dead limbs of the koa trees in the mountain forests.

Mr. S. B. Wilson remarks:

Nature has shown great symmetry in regard to the species of this genus (*Hemignathus*) to be found in the Sandwich Archipelago, three of the main islands having each a long-billed and a short-billed form.

This of course is most natural. Both long-billed forms (*Hemignathus*) and short-billed forms (*Heterorhynchus*) have spread from the island where they were originally developed to the other islands, each changing as it is isolated from the main body of the species and subjected to natural selection under new conditions.

With the genus *Hemignathus* and its aberrant section, *Heterorhynchus*, the

forms with slender bills reach their culmination.

Going back to the original stock, to which *Oreomystis bairdi* is perhaps the nearest living ally, we note first a divergence in another direction. In *Rhodacanthus*, the bill is stout like that of the large finch, not longer than the rest of the head, and curved downward a little at the tip. The species of this genus feed largely on the bean of the acacia and other similar trees, varying this with caterpillars and other insects. The stout bill serves to crush the seeds. In *Chloridops*, the bill is still heavier, very much like that of a grosbeak. *Chloridops kona* is, according to Mrs. Robert Perkins, a dull sluggish solitary bird and very silent, its whole existence may be summed up in the words 'to eat.' Its food consists of the fruit of the aaka (bastard sandal tree), and as they are very minute, its whole time seems to be taken up in cracking the extremely hard shells of the fruit, for which its extraordinarily powerful bill and heavy head have been developed.

The incessant cracking of the fruits, when one of these birds is feeding, the noise of which can be heard for a considerable distance, renders the bird much easier to get than it otherwise would be. Its beak is always very dirty with a brown substance adhering to it which must be derived from the sandal-nuts.

In *Psittirostra* and *Pseudonestor* the bill suggests that of a parrot rather than that of a grosbeak. The mandibles are still very heavy, but the lower one, as in *Heterorhynchus*, is short and straight, while the much longer upper one is hooked over it. *Pseudonestor* feeds on the larvæ of wood boring beetles (*Clytanus*) found in the koa trees (*Acacia falcata*), while the closely related *Psittirostra* eats only fruits, that of the ieie (*Freycinetia arborea*), and the red mulberry (*Morus sapyrifera*) being especially chosen. In all these genera

there is practically a species to each island, except that in some cases the species has not spread from the mountain or island in which we may suppose it to have been originally developed.

There are a few other song birds in the Hawaiian Islands, not related to the Drepanidæ. These are derived from the islands of Polynesia and have deviated from the original types in a degree corresponding to their isolation.

In the case of the Drepanidæ it seems natural to conclude that natural selection is responsible for the physiological adaptations characteristic of the different genera. Such changes may be relatively rapid, and for the same reason they count for little from the standpoint of phylogeny. On the other hand, the non-useful traits, the petty traits of form and coloration which distinguish a species in Oahu from its homologue in Kauai or Hawaii, are results of isolation. These results may be analyzed as in part differences in selection with different competition, different food and different conditions, and in part to hereditary difference due to the personal eccentricities in the parent stock from which the newer species was derived.

In these and in all similar cases we may confidently affirm: The adaptive characters a species may present are due to natural selection or are developed in connection with the demands of competition. The characters, non-adaptive, which chiefly distinguish species do not result from natural selection, but from some form of geographical isolation and the segregation of individuals resulting from it.

The origin of races and breeds of domestic animals is in general of precisely the same nature. In traveling over England one is struck by the fact that each county has its own breed of sheep, each of these having its type of excellence in mutton, wool, hardiness or fertility, but

the breeds distinguished by characters having no utility either to sheep or to man.

The breeds are formed primarily by isolation. The traits of the first individuals in each region are intensified by the in-breeding resulting from segregation. Natural selection preserves the hardiest, the most docile and the most fertile; artificial selection those which yield the most wool, the best mutton and the like. The breed once established, artificial selection also tends to intensify and to preserve its non-adaptive characteristic marks. The more pride the breeders take in their stock, the more certain is the preservation of the breed's useless peculiarities.

Taking the common middle-wool sheep of southern England, the following key to some of the visible race traits was made while driving along the county roads.

- a. Rams and ewes with short white horns. Dorsetshire.
- aa. No horns.
- b. Face and ears black.
- c. Skin below tail black. Hampshire.
- cc. Skin below tail white. Devonshire.
- bb. Face and legs tawny; no black. Southdown.
- bbb. Face and ears white; ears erect. Cheviot.

Not one of these characters has the slightest intrinsic or physiological value. Each of them would disappear in a few generations of crossing, and in each breed the virtues of wool or of flesh exist wholly independently of these race marks.

Analogous to these race peculiarities of sheep are the minor traits among the men of different regions. Certain gradual changes in speech are due to adaptation, the fitness of the word for its purpose, analogous to natural selection. The non-adaptive matters of dialect find their origin in the exigencies of isolation, while languages in general are explainable by the combined facts of migration, isolation and the adaptation of words for the direct uses of speech.

In the animal kingdom generally we may say: whenever a barrier is to some extent traversable, the forms separated by it are liable to cross from one side to the other, thus producing intergradations, or forms more or less intermediate between the one and the other. For every subspecies, where the nature of the variation has been carefully studied, there is always a geographical basis. This basis is defined by the presence of some sort of a physical barrier. It is extremely rare to find two subspecies inhabiting or breeding in exactly the same region. When such appears to be the case, there is really some difference in habit or in habitat; the one form lives on the hills, the other in the valleys; the one feeds on one plant, the other on another; the one lives in deep water, the other along the shore. There can be no possible doubt that subspecies are nascent species, and that the accident of intergradation in the one case and not in the other implies no real difference in origins.

Of all branches of science, we may say that the one most advanced in its development, most nearly complete in its conclusions, is that of the systematic study of American birds. No other group of naturalists has made such extensive studies of individual or of group variations as the ornithologists who have dealt with American birds. And for this reason, and on account of the excellence of the preserved material with which they have to deal, the students of our birds have thoroughly understood the relation between species-making and geographical distribution, the persistence of group variation and the origin of species.

While the processes of natural selection may be always at work destroying those individuals not fitted to their surroundings, and accentuating the adaptation of the species through those which survive, and while

sometimes natural selection may work with great acceleration where conditions are widely changed, yet it is clear that the characters by which one species is actually known from the next are rarely traits of utility. Such traits bear no visible relation to the process of natural selection, using that term in a strict sense.

For example, we may compare the species of American orioles constituting the genus *Icterus*. We may omit from consideration the various subspecies, set off by the mountain chains, and the usual assemblage of insular forms, one in each of the West Indies, and confine our attention to the leading species as represented in the United States.

The orchard oriole, *Icterus spurius*, has the tail all black, the head all black, the lower parts chestnut, and the body relatively small, as shown by the average measurements of different parts. In the hooded oriole, *Icterus cucullatus*, the head is orange, the throat black, and the wings are black and white. This species, with its subspecies, ranges from Southern California over much of Mexico. Our other orioles have the tail black and orange. In the common Baltimore oriole, *Icterus galbula*, of the east, the head is all black, and the outer webs of the wing coverts are black and white. In the equally common bullock oriole, *Icterus bullocki*, of the California region, the head is partly yellow, and the greater wing coverts are mostly black. The females of all the species are plain olivaceous, the color and proportions of parts varying with the different species, while in the males of each of the many species black, white, orange and chestnut are variously and tastefully arranged. Each species again has a song of its own, and each its own way of weaving its hanging nest.

That which interests us now is that not one of these varied traits is clearly related

to any principle of utility. Adaptation is evident enough, but each species is as well fitted for its life as any other, and no transposition or change of the distinctive specific characters or any set of them would in any conceivable degree reduce this adaptation. No one can say that any one of the actual distinctive characters or any combination of them enables their possessors to survive in larger numbers than would otherwise be the case. One or two of these traits, as objects of sexual selection or as recognition marks, have a hypothetical value, but their utility in these regards is slight or uncertain. It is customary at present to look with disfavor on sexual selection as a factor in the evolution of ornamental structures, and the psychological reality of recognition marks is yet unproved, though not at all improbable.

It may be noted, in passing, that the prevalent dull yellowish and olivaceous hues of the female orioles of all species is clearly of the nature of protective coloration.

Professor Vernon L. Kellogg has shown statistically that certain specific characters among insects have no relation to the process of selection. Among honey bees the variation in venation of the wings and in the number and character of the wing hooks is just as great when the bees first come from their cells as in a series of individuals long exposed to the struggle for existence.

Among ladybird beetles of one species (*Hippodamia convergens*) 84 different easily describable 'aberrations' or variations in the number and arrangement of the black spots on the wing covers have been traced. These variations are again just as numerous in individuals exposed to the struggle for life as in those just escaped from the pupal state. In these characters there is, therefore, no rigorous

choice due to natural selection. Such specific characters, without individual utility, may be classed as indifferent, so far as natural selection is concerned, and the great mass of specific characters actually used in systematic classification are thus indifferent.

And what is true in the case of the orioles is true as a broad proposition of the related species which constitutes any one of the genera of animals or plants. All that survive are well fitted to live, each individual, and therefore each species fitted to its surroundings as the dough is to the pan, or the river to its bed, but all adaptation lying apparently within a range of the greatest variety in non-essentials. Adaptation is the work of natural selection: the division of forms into species is the result of existence under new and diverse conditions.

To the general rule that closely allied species do not live together there exist partial exceptions. It may be well to glance at some of these, for no rule is established until its exceptions are brought into harmony with the phenomena which illustrate the rule.

The most striking case of this sort known to us is that of the Pescado Blanco of the volcanic lakes of Mexico, these constituting the genus *Chirostoma* in the family of Atherinidæ.

In the large lake of Chapala in central Mexico, tributary to the Rio Lerma, one species, *Chirostoma estor*, has been known for years. It is a pale, translucent fish of elongate form, about fifteen inches in length, with very delicate flesh, and it is much appreciated as a food fish under the local name of 'Pescado Blanco de Chapala.' In a recent visit to that region, the Pescado Blanco was found to be abundant in the lake, but to the great surprise of the writer, in the same catch of the net were found

under the same general guise of size and appearance some half a dozen distinct but closely related species of Pescado Blanco. In each case the different species most nearly related seemed to be found together, an exception to the rule otherwise almost universal among animals and plants. Later explorations of Dr. Seth E. Meek in this and other lakes confirmed and magnified this anomaly. The genus *Chirostoma* is confined to the lakes of the tablelands of Mexico. It includes three groups or subgenera: *Chirostoma* proper, green in color and with firm, smooth scales; *Lethostole*, with smaller scales, rough edged, the body white or translucent, and *Eslopsarum*, of smaller species, also white, but with still larger scales, larger than in *Chirostoma* or *Lethostole*. The species were found to be grouped as follows:

Lake Chapala.	{	(<i>Lethostole</i>) <i>estor</i> .
		(<i>L</i>) <i>ocotlanæ</i> .
		(<i>L</i>) <i>termæ</i> .
		(<i>L</i>) <i>sphyræna</i> .
		(<i>L</i>) <i>lucius</i> .
		(<i>L</i>) <i>promelas</i> .
		(<i>L</i>) <i>grandocule</i> .
		(<i>L</i>) <i>chapalæ</i> .
Lake Patzcuaro.	{	(<i>Eslopsarum</i>) <i>labarcæ</i> .
		(<i>E</i>) <i>bartoni</i> .
		(<i>L</i>) <i>estor</i> .
		(<i>L</i>) <i>grandocule</i> .
		(<i>Chirostoma</i>) <i>humboldtianum</i> .
Lake Zirahuen.	{	(<i>E</i>) <i>patzcuaro</i> .
		(<i>E</i>) <i>attenuatum</i> .
		(<i>L</i>) <i>estor</i> .
Lake Chalco (City of Mexico).	{	(<i>E</i>) <i>ziráhuen</i> .
		(<i>C</i>) <i>humboldtianum</i> .
		(<i>E</i>) <i>jordani</i> .
Aguas Calientes.	{	(<i>E</i>) <i>arge</i> .

No data exist for the explanation of this peculiar case of distribution. It is possible that *C. humboldtianum* of the lakes of Mexico represents the ancestral type, that the

groups *Eslopsarum* and *Lethostole* have diverged from it, and that the numerous species of the last-named type in the large lakes, Chapala and Patzcuaro, have been formed by mutations in the sense of the use of the word by de Vries. But it is possible that these species have been formed by isolation, and that species thus formed have invaded the territory of other species. The shifting of the shores of these volcanic lakes and of the hydrographic basins to which they belong is among the possible causes to be considered.

Another curious case of the occurrence in one locality of similar species is found in the genus *Eviota* of the family of Gobiidae or gobies.

Eviota contains very minute fishes of the coral reefs, translucent green in color, plain or blotched with orange and marked with black spots. One species one and a half inches long (*Eviota abax*) is found in Japan, and one an inch long (*Eviota personata*) in the West Indies. The other species are all less than an inch in length, some of them but half an inch, perhaps the smallest of all vertebrate animals. One of these, *Eviota epiphanes*, is found in crevices in the coral reefs of Hawaii. Another, *Eviota miniata*, is recorded from Guam. All the remaining species, including those most closely related, are known only from the crevices of coral heads in Samoa. Most of the known specimens, hundreds in all, were obtained by the writer and his associates in Apia and Pago Pago. Our native assistants would dive for these coral masses, and on cracking them, the little fishes would be found in their channels and interstices. In Samoa the following species occur: *Eviota zonura*, *E. smaragdus*, *E. prasites*, *E. afelei*, *E. sebreei*, *E. pruinosa*, *E. herrei*, *E. distigma*. It would seem as if these species could not have had a geographic origin in the ordinary sense, for they are all grouped

together in the same neighborhood. It is, however, possible that the isolation of a part of the reef or even of that of a single coral head might in long periods serve the same purpose.

Enneapterygius is a genus of blennies in size and distribution closely parallel with *Eviota*. It contains species of moderate size found in the Gulf of California, in New Zealand, the Red Sea and Japan. In these same coral heads, species of this genus also occur, all of them extremely minute, much smaller than their relatives in other waters, and scarcely larger than the species of *Eviota*, among which they live. These minute fishes are mostly red in color, sometimes partly black. Again one species (*Enneapterygius atriceps*) is found in the Hawaiian reefs, and again six species (*E. minutus*, *E. hemimelas*, *E. hudsoni*, *E. tusitala*, *E. cerasinus* and *E. tutuila*) live together in the coral heads of Samoa.

The more usual distribution of a group of closely related fishes may be shown by the group of silver-fin minnows, the section *Erogala*, in the genus *Notropis* among the fishes.

All these are small minnows, with large scales, and with the dorsal fin marked by a large black blotch on its last rays above. This fin in the males is tipped with a broad stripe of silvery or milk-white pigment, and sometimes also shaded with bright red, orange or blue, very conspicuous in the breeding season.

The simplest, most primitive and most widely distributed form is *Notropis whipplii* of the Mississippi Valley. Near to this in the Upper Tennessee is *Notropis galacturus*. In the Ozark range is *Notropis camurus*. Farther south a black spot appears at the base of the tail. This marks *Notropis notatus* in the Rio Colorado of Texas, *Notropis venustus* in the Rio

Sabinal, *Notropis cercostigma* in Pearl River, and *Notropis stigmaturus* in the Alabama. On the eastern part of its range, the nearest relative of *Notropis whipplii* is *Notropis analostanus* of the Potomac. Near to this is *Notropis niveus* of the North Carolina rivers and *Notropis chloristius* of the Santee. Other variants from these are *Notropis eurystomus* of the Chattahoochee, *Notropis xanurus* of the Allamaha, *Notropis caeruleus*, *callistius* and *trichroistius* of the Alabama and Black Warrior, the last two with scarlet on the dorsal. Finally come the most specialized extremes, *Notropis pyrrhomelas* of the Santee and *Notropis hypselopterus* of the Mobile. Each southern river has one or more species of this type, and the streams of Georgia have been invaded from the north and from the west, the two types meeting in the basin of the Alabama.

In the little group of minnows called *Hydrophlox*, another section of the genus, *Notropis rubricroceus*, and its allied species, scarlet, black and golden, are distributed in precisely the same fashion, and about the same number of species are developed. Those found in the Mississippi River have the widest range of distribution and the least specialization in their traits. Those in the clear waters of the southern slope of the Blue Ridge are most intensely colored, most specialized in the traits, and show the narrowest range in distribution.

If fishes were as easily preserved, measured and examined as birds, and if they were studied by as many keen eyes, we might find perhaps that each of these species is again broken up into races or subspecies, their traits determined in some degree by their individual parentage, in larger part by the local selection they have undergone in their diverse waters and surroundings. This is certainly probable in

the case of fresh-water fishes, but with marine fishes there is greater freedom of migration, the species are perhaps largely of more ancient origin and intergrading forms are much more rarely recognized.

The degree of fulness and accuracy in the recognition of subspecies marks the degree of progress in any branch of systematic or of faunal zoology and botany. It is the tyro who, as Linnæus² suggests, sees the problems of geographical distribution in the large. It is the master who follows step by step the footprints of the Creator in the molding and distribution of life.

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SCIENTIFIC BOOKS.

The Waterlilies: A Monograph of the Genus Nymphaea. By HENRY S. CONARD, Senior Harrison Fellow in Botany, University of Pennsylvania. Published by the Carnegie Institution of Washington. 1905. Pp. xiii + 279. 4to, 30 plates and 82 figures in the text.

This thick volume, which is listed as 'Publication No. 4' of the Carnegie Institution of Washington, appeared several months ago, and attracted immediate attention on account of its excellence of paper, type, presswork and plates. In the style of its publications the institution is setting a high standard which can not but favorably affect scientific publication throughout the country. The plates are from drawings (some colored) and photographs, which have been very faithfully reproduced. The text-figures, while largely outlines, are also well done, adding greatly to the value of the work.

Turning now to the text, we find a chapter given to a historical sketch, followed by another devoted to structure, still another to development, one to physiology. The central chapter devoted to taxonomy is the longest and most important, and this is followed by brief discussions of distribution, hybrids and

garden varieties, culture and uses and an extended bibliography. From the preface we learn that 'nothing like a complete synopsis of the waterlilies has hitherto been put before the English-speaking world,' and indeed it appears that it is more than eighty years since the last complete treatment in any language, *i. e.*, De Candolle's in the 'Prodromus' (1824). The present work is the result of studies undertaken by the author in the botanical garden and laboratories of the University of Pennsylvania, supplemented by living and preserved specimens and material from many sources, including that in the herbaria in Kew, British Museum, Linnean Society, Berlin, Munich, etc.

It would be pleasant to summarize, or quote from the historical chapter in which many interesting facts are brought together in very readable form. Likewise there is much of interest and importance in the chapter on structure, which includes gross and minute anatomy, and in the next chapter on the physiology of the plants (including a discussion of the cause of the opening and closing of the flowers), but there is no space here for this. The reader is recommended to peruse the interesting chapters for himself.

The chapter on taxonomy is the one of most general interest to the ordinary reader. The author prefers the name *Nymphaea* to *Castalia* for the genus, reserving the latter for one of the subgenera. The species are arranged under two principal groups, viz., (I.) *Nymphaeae Aprocarpiae* (with carpels free from one another at the sides) and (II.) *Nymphaeae Syncarpiae* (with carpels completely fused with one another at the sides). Two subgenera are recognized in the first group, *Anecphyra*, with but one species, *N. gigantea* (Australian), and *Brachyceras*, with twelve species, *N. elegans* (Texas and Mexico), *N. ampla* (tropical and subtropical America) *N. flavo-virens* (probably Mexican), *N. stellata* (southeast Asia), *N. coerulea* (Africa), *N. micrantha* (West Africa), *N. heudelotii* (Africa), *N. ovalifolia* (East Africa), *N. calliantha* (Africa), *N. capensis* (South Africa), *N. sulfurea* (Africa), and *N. stahlmannii* (Africa). In the second group the subgenus *Castalia* in-

² "Tyro fit classes: magister fit species."