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ARTICLE VIII.

ON THE LOCAL DISTRIBUTION OF CERTAIN ILLINOIS FISHES : AN
ESSAY IN STATISTICAL ECOLOGY.

BY

S. A. FORBES, Ph.D.

ERRATA AND ADDENDA.

- Page 55, line 15, for 1854 read 1855.
Page 55, line 16, for *Horticultural* read *State Agricultural*.
Page 60, in second table, Illinois, for 240 read 241.
Page 65, first line above foot-note, for *ventricosa* read *ligamentina*.
Page 72, line 9, for *imbecilis* read *imbecillis*.
Page 79, line 19, for *asperimus* read *asperrimus*.
Page 80, above *Quadrula rubiginosa* insert Section *Fusconaia* Simpson.
Page 76. The record of Calkins for *Margaritana margaritifera* is without doubt erroneous and should be eliminated. This species is not found in Illinois.
Page 95. *Pomatiopsis sheldonii* Pilsbry should read *Ammicola sheldonii* and should be transferred to the genus *Ammicola* on page 93.
Page 100. *Physa gyrina oleacea* Tryon is the immature stage of *Physa gyrina*.
Page 103. *Lymnaea tazewelliana* is a synonym of *Lymnaea parva*.
Page 105. *Lymnaea palustris michiganensis* is the immature form of *Lymnaea reflexa*.
Page 106. *Lymnaea reflexa iowensis* and *Lymnaea reflexa crystalensis* are synonyms of *Lymnaea reflexa*.
Page 112, line 6 from bottom, for *gouldi* read *gouldii*.
Page 114, line 5 from bottom, for *juxtigens* read *juxticens*.
Page 115, line 21, for *Witter* read *Walker*; line 23, *Polygyra sayii* Binney should be changed to *Polygyra sayana* Pilsbry.
Page 116, line 1. *Polygyra exoleta* Binney (1885) should be changed to *Polygyra zaleta* Binney (1837).
Page 117, line 11 from bottom, for *leai* read *leaii*; line 3 from bottom, *Polygyra monodon fraterna* is a good species and should read *Polygyra fraterna*.
Page 119, foot-note. A specimen of *alliaris* in the collection of Mr. Aldrich, received from Calkins, proves to be *draparnaldi*.
Page 121, line 3 from bottom, for *Champaign* read *Piatt*.
Page 122, line 12 from bottom, for *Pyramidula striatella* Anthony read *Pyramidula cronkkitei anthonyi* Pilsbry; line 4, for *Held* read *Hald*.
Page 123, for *Helicodiscus lineatus* Say read *Helicodiscus parallelus* Say.
Page 162, line 7, for *glandulosa* read *linearis*.
Page 171, line 17, for *riparia* read *vulpina*.
Page 176, line 8 from bottom, for *canadense* read *majus*.
Page 180, line 9, for *virginica* read *virginiana*.
Page 221, line 6 from bottom, for *rectangulus* read *rectangularis*.
Page 226, line 3, for *fasciatus* read *fasciata*.
Page 239, line 11, strike out Lake Co. entry.
Page 246, lines 6 and 7, and page 248, lines 1, 14, 20, and 23, for *Enothera* read *Onagra*.
Page 248, line 4, for *candida* Horn substitute n. sp.

Page 249, line 8 from bottom, for *Olethreutes dimidiana* Sodoff? read *Olethreutes separatana* Kearfott, and strike out parenthetical matter.

Page 251, line 7, for *grossa* read *thoracica*; line 21, for words preceding H. 6, read *Asilus rufipennis* Hine; line 18 from bottom, for words preceding H. 2, substitute *Asilus cacopilogus* Hine.

Page 253, line 8, for *Linn.* read *Emory*.

Page 257, line 15, for *pennsylvanicus* DeG. read *auricomus* Rob.

Page 261, Note 6. *Melanoplus macneilli* is very probably *M. fluviatilis* Brun.

Page 262, Note 9. Dr. Bergroth writes that *Nabis elongatus* is preoccupied. The original is *elogantus* in the check list. Comparison with long-winged *vicarius* is desirable before re-naming it.

Page 309, in table, for 59 read 57, and for 743 read 741.

Page 310, in table, for 59 read 57.

Page 314, line 5, for 1587 read 481; line 16, after *stubble* insert *meadows*; line 17, after *pastures* strike out *and meadows*, and after 1500 strike out *each*.

Page 315, last line, for 553 read 481.

Page 362, line 7 from bottom, for *longa* read *parvilamellata*.

Page 373. As a second entry in synonymy insert as follows:

1854. *Nothrus bistriatus*, Nicolet, *Acariens des Environs de Paris*, p. 397, Pl. VII., Fig. 7.

Page 376, line 13 from bottom, for *Oribata* read *Oribates*.

Page 378, line 1, for XXV. read XXXV.

Page 384, after line 5 insert as follows:

N. bipilis Hermann. *Mem. Apt.*, p. 95.

In moss, Arcola and Parker, Ill.

Page 384, line 5 from bottom, for *pyrostigma* read *pyrostigmata*.

Page 386, after line 11 from bottom insert as follows:

H. bistriata Nicolet. *Acariens des Environs de Paris*, p. 397, Pl. VII., Fig. 7.

Under logs and in moss, Urbana and Arcola, Ill.

Page 388, line 12, for *sphærum* read *sphærule*.

ARTICLE VIII.—*On the Local Distribution of certain Illinois Fishes: an Essay in Statistical Ecology.* BY S. A. FORBES.

An animal society is composed of animals habitually occurring together in the same locality and the same class of situations. Such an association is, of course, composed of many species, variously related to their special environment, some attracted to it by one set of conditions and some by another. Although their local haunts may be virtually identical, their ecological relations, if determined in detail, may prove to be very different. A pike and a minnow may be members of the same associate group, to whose habitat, however, the pike is especially attracted by the minnow, and the minnow by the facilities which are offered there for concealment or escape from the pike.

It is usually possible to learn the contents of a local association of plants by simple inspection and enumeration; but animals come and go, elude observation, and refuse to be numbered, and the details of their associate occurrence can only be learned indirectly, by means of sample collections preserved for subsequent study. If the situations from which such collections are made are carefully chosen and correctly classified, and if the collections themselves are full enough, uniform enough, and numerous enough to be fairly representative of each situation, the essential facts concerning the assemblage of animals corresponding to any unit of environment may be readily made out. The making of such collections for such a purpose is, however, a relatively new thing, and scarcely a beginning has been made in the systematic study of animal associations by this method.

A knowledge of definitely circumscribed, or merely measurably distinct, local associations does not, however, by any means exhaust the subject of associate relations, for the animals of a region can not be wholly divided up into such definite

societies, and such society groups as can be clearly recognized rarely have any precise boundaries. For a full knowledge of the intricate web of the relations to their physical environment, and through that to each other, of the animals of any composite area, it is necessary that the entire assemblage of the inhabitants of that area should be studied as a compound unit, and for this, of course, extensive and comprehensive collections must be made, such as will fairly represent the entire animal life of their region.

The possession of a miscellaneous but very large collection of Illinois fishes, obtained during various seasons of a long period of years, from all kinds of waters and in all parts of the state (see Map I.), each lot still bearing, as a rule, the original collector's data giving both the time of collection and the exact locality, has suggested to me a trial study, intended to show what may be learned with regard to the ecology of fishes by a critical analysis of the local data of such a collection.

These data may be organized and generalized for ecological study in two ways. They may be treated in one mass, without local subdivision, and in such a way as to bring out the facts concerning the association of the different species of fishes with each other, without reference, in the first instance, to the localities and situations from which the specimens have been taken; or they may be first divided and arranged according to location and surroundings, the assemblage of species from each geographical unit and from each kind of ecological situation being studied separately, as a local animal society. The first method has the advantage over the second, that it gives us much larger numbers of specimens and collections from which to generalize, and thus enables us to enter further into the details of the associate relationship without danger of error from unsafe generalization; and it also enables us to distinguish similarities and differences of ecological relationship among the species, uninfluenced by any previous discrimination or classification of ecological situations. The second method has the advantage over the first, that it attacks the problem more

simply and more directly, and, if the data are sufficient, reaches results more immediately and obviously significant.

I have used both these methods in the present paper, comparing the results of the two in a way to make the one set account for and explain the other. This paper is thus to be taken as a contribution to an answer to the following questions: What Illinois fishes are habitually found in each others' society, and what is the relative frequency of their associations? How are Illinois fishes grouped and distributed according to location and situation, and in each ecological assemblage so formed what is the proportionate representation of its various constituent species? How far are the two classes of data, those of associative affiliation and of ecological relationship, comparable, and to what extent may the one be used to explain the other? An answer to these inquiries would enable us to recognize, define, and account for associate groups among our fresh-water fishes, and also to distinguish those members of each group which, being most frequently and most strictly associated, are most characteristic of it. It has, in fact, been a part of my undertaking to find a method of distinguishing clearly these central or typical members of an ecological assemblage, and to express numerically the intensity of the influence—the strength of the bond—which holds them to the local situation, as compared with the more lax or less continuous forces influencing what we may call the outlying members of the group.

Studies of this description may be expected to give us significant information, also, concerning the competitions of associated species, and concerning the evasions of competition, and the escape from its consequences, by those closely related and similarly endowed, and concerning the niceties of adaptation, psychological, physiological, and structural, exhibited by fishes inhabiting a notably uniform area.

ASSOCIATIVE RELATIONSHIPS AMONG THE ETHEOSTOMINÆ.

For a preliminary and sample study of this description, I have chosen first a subfamily of our fishes, the *Etheostomine*—or darters, as they are commonly called—and have endeavored

to learn to what extent the species of this subfamily are ecologically affiliated, which of the species are most typical of the subfamily as an ecological group, which are to be regarded as lagging or wandering members of it, and which, if any, do not belong ecologically with their taxonomic relatives.

I shall be obliged, in these studies, to assume provisionally that my collections are large enough and numerous enough fairly to represent actual field conditions in Illinois, and that they are so numerous that they may reasonably be treated, for the present purpose, as homogeneous and similar, each collection as a unit substantially like every other, important differences among them disappearing, in aggregates and averages, by the process of mutual cancelation. In other words, I must assume provisionally, testing my supposition later by the constancy and reasonableness of the results, that these random samples of Illinois darters represent the subfamily as a whole sufficiently well to justify their use as materials for a study in statistical ecology.

THE METHOD OF THE INVESTIGATION.

The species of darters which are most frequently found in each others' company are, of course, those most likely to be closely related ecologically; and the ratio of the number of collections containing both of any two species to the total number of collections containing either, may be used as a provisional measure of the ecological affinity of the two.

Furthermore, given a certain average frequency of occurrence of each of two species inhabiting a common territory, and assuming a uniform distribution of each in this territory, uninfluenced by ecological relationships, the average frequency of the joint occurrence of these species in collections may be computed; and any very marked departure, positive or negative, from this computed average will point to some ecological bond if the difference is positive, or to some cause of ecological separation if it is negative.

If, for example, it appears that several species ought to be found together, on an average, in one out of twenty of our col-

lections, provided that they are distributed over their common area uninfluenced by causes tending to bring them together into the same situations, and if the actual average of the joint occurrences of the species is one in every five collections, then the associative bond of the species concerned may be given the value of four—a value of little significance perhaps, taken by itself, but useful, at any rate, for a comparison of the darters with other groups. And if certain of the species are associated with the other darters in an average ratio of five to one, while other species are associated with the other darters in an average ratio of only two to one, then the former species will typify the ecological group more definitely and correctly than the latter.

By this means, also, if the actual frequencies of joint occurrence of the various species of the group be compared with the computed average of such frequencies, the division of any presumably single group into two distinguishably separate ones might be made out. If it should appear, for example, that the species of darters may be divided into two groups, each of which taken separately is found to have a mutual associative ratio of six to one, while the corresponding ratio between the two groups themselves is but three to one, we may infer provisionally the division of the darters into two ecological groups, distinguishable by their predominant attraction to different sets of ecological factors in their common environment, but united in turn in one larger group by their common attraction to certain other factors.

For an analysis of the facts, we need for each species of darter a determination of the average frequency of its merely chance occurrence in collections with each of the other species, a determination of the actual frequency of these joint occurrences, and a numerical expression of the ratio of one of these frequencies to the other. Then by a systematic tabulation of these latter ratios, which may be called the *coefficients of association*, we may compare one species with another, and bring the essential data for the whole family under the eye for convenient inspection and analysis.

For the computation of these ratios, I have used, with two exceptions to be presently stated, the thousand Illinois collections most available for these studies, excluding five hundred and forty-four additional collections, which, because of imperfect data and for various other reasons, are undesirable material. I find that the species *Hadropterus aspro* has been taken in 159 of these thousand collections, which ratio of average frequency may be expressed by the fraction .159; and that the species *Hadropterus phoxocephalus* has been taken 85 times, which gives a frequency ratio of .085. That is, in any thousand similar miscellaneous collections distributed over the area inhabited by these species we may, according to these data, expect to get the first species 159 times and the second species 85 times; and the chance that any single collection will contain the first species is .159, and that it will contain the second species is .085. From this it follows that the chance that the two species will occur together in any single collection of the thousand, provided that the distribution of each is arbitrary and accidental with reference to that of the other, is the product of these fractions; and the probable number of chance joint occurrences of the two species in the thousand collections is, of course, a thousand times that product, or 13.515. As a matter of fact, however, these two species were found together in my collections 40 times instead of approximately 13.5 times, or three times as frequently as there was reason to expect provided that there had been no associative bond between the species. This number 3, indicative of the frequency of actual association as compared with the chance or accidental, is the coefficient of association for these two species. If the numbers of presumable and actual joint occurrences were equal, this coefficient would evidently be 1, in which case no associative bond would be indicated; and if it were notably less than 1, we should have some reason to suppose that the two species belonged to different ecological groups—that their ecological affinities and relationships tended to separate them instead of to bring them together.

The computation may be facilitated by the use of algebraic symbols.

Let a equal the total number of collections to be used in the computation; b , the number of collections containing the more abundant of two species to be compared with one another; c , the number of collections containing the less abundant of these species; and d , the number of collections each of which actually contains both species together. Then $\frac{b}{a}$ expresses the chance that any collection of a will contain one or more representatives of the first species; $\frac{c}{a}$, the chance that any collection will contain one or more representatives of the second species; $\frac{bc}{a^2}$, the chance that any collection will contain one or more representatives of both species at once, provided that the distribution of each is ecologically independent of that of the other; and $\frac{bc}{a}$, the probable number of chance occurrences of the first and second species together in the number of collections represented by a , the same proviso being made. Since $d =$ the actual number of such joint occurrences, $\frac{ad}{bc}$ is the formula for the ratio of actual to calculated joint occurrences—the formula, in other words, for the computation, in all cases, of our coefficients of association. For example, substituting in this formula the values already given for *Hadropterus aspro* and *Hadropterus phorocephalus*,

$$\frac{ad}{bc} = \frac{1000 \times 40}{159 \times 85} = 2.96.$$

To determine the coefficient for any pair of species, we need only to know their separate frequencies and their joint frequencies in collections derived from the territory of their common distribution.

The above formula may be translated into the following rule for finding the coefficient of association of any two

species: *Multiply the number of collections made from the common area of the species by the number containing one or more representatives of both; multiply the number of collections containing one or more representatives of one of the species by the number containing one or more of the other; and divide the first product by the second. The quotient will be the coefficient of association.*

DISCUSSION OF ASSOCIATIVE TABLES.

I have computed, by the above-described method, for thirteen species of Illinois darters—each of which was obtained more than fifteen times in my collections—the coefficients of the association of each species with each of the other twelve, and have arranged these seventy-eight coefficients (apparently one hundred and fifty-six, since each of them is entered twice) in Tables I.-V. for comparison and discussion. In computing the coefficients of two species, *Diplesion blennioides* and *Etheostoma zonale*, the first of which is found only in the eastern part of the state and the second only in the northern half, I have used as the value of a in my formula, not the entire number of collections made throughout the state, but the number made in the stream systems in which these species occur.

In Table I. the coefficients in each column are in serial order, the highest to the lowest from above downwards; and the columns for the several species are placed in the order of the average coefficients for the columns, the highest at the left.

We notice first, that the total of the one hundred and fifty-six coefficients of this table is 315.8—a general average associative coefficient of 2.02 for all the thirteen species. As the normal chance average would be but 1, we conclude, from these data, that darters were found together in my collections about twice as frequently as mere chance would indicate. This ratio of 1 to 2 is thus an approximate and provisional measure of the ecological bond in this family taken at large.

We notice next, the unlike totals and averages of the coefficients for the several species, these running from 1.22 to 2.69—an indication that the associative bond is more than 2.2 times as strong for *Hadropterus phoxocephalus* and *Etheostoma*

zonale as for *Boleichthys fusiformis* and *Boleosoma camurum*. On the other hand, we find no species in which the average coefficient of association is less than 1—no indication that any of these twelve species are wholly drawn away from their family by stronger ecological affiliations with some other group. Nor do we find, in passing from the more strongly associated species to those less strongly associated, any abrupt transition in the series—a fact which may be taken as evidence that the darters of my list are a unitary group, of which certain species are ecologically more typical than others, having, that is, the darter habits and relationships more fully developed and more strongly fixed.

TYPICAL AND NON-TYPICAL DARTERS.

The more typical species of this list seem to be the following six, mentioned in the order of the size of their coefficients of association: *Hadropterus phoxcephalus*, *Etheostoma zonale*, *Etheostoma flabellare*, *Hadropterus aspro*, *Ammocrypta pellicida*, and *Etheostoma ceruleum*, the associative coefficients of which average 2.48. Apparently the least stringently connected with their kind by the associative relation are *Diplesion blennioides*, *Etheostoma jessie*, *Boleosoma camurum*, and *Boleichthys fusiformis*, the average coefficient of which is 1.36.

Furthermore, those least strictly associated with darters in general are not especially strongly associated with each other. Of the four species just mentioned, six pairs may of course be made, and the average of the coefficients of these six pairs is 1.33—less by .69 than the general average for the entire group (see Table III.). If we similarly pair the six species which I have selected as most typical, and average the fifteen coefficients of these pairs (see Table IV.), we get a general coefficient of 3.47—more by 1.5 than the average for the group. That is, those species which are laxly associated with the darters in general, are also laxly associated with each other; while those which are strongly associated with darters in general, are still more strongly associated among themselves. This last fact was to be anticipated, since in making up the special average coeffi

cients of those species which exhibit strong associative affinities we omit those which have the weaker affinities, and so have a group of select associates whose average coefficient must be higher than that of the whole thirteen species, including, as this does, some with strong and others with feeble associative tendencies.

The same fact is illustrated in Table II., in which all the coefficients of the seventy-eight possible pairs of my thirteen species are arranged in the order of the magnitude of their coefficients of association with *Hadropterus aspro* (1421). Taking the first twenty-one coefficients of the six most frequent associates of *Hadropterus aspro*, we find that they average 3.27, while the last twenty-one coefficients of the six least frequent associates of *Hadropterus aspro* average 1.4. That is, the twenty-one coefficients at the upper left angle of Table II. (above the black line) average two and a half times as much as the twenty-one coefficients at the lower right angle of that table (to the right of the black line). The most frequent associates of this species are associated with each other about two and a half times as frequently as are its least frequent associates.

It is also significant that five of the list of six most frequent mutual associates made up from Table I., are the same as those of the corresponding list made up from Table II., of *Hadropterus aspro* and its five closest associates, the two tables containing the same figures, differently arranged. We further notice that the three least frequently associated species are the same on both lists. Whether the data indicating frequency of association are arranged under each species independently, in the order of frequency, as in Table I., or with reference only to a single leading species, as in Table II., the results are nearly identical as to the darters most typical and least typical of the group.

SUFFICIENCY OF THE COLLECTIONS.

With respect to the sufficiency of the collections for the use which is here made of them, some additional evidence may be found by tabulating separately the seven species which appear least frequently in them—ranging in number of occurrences

from 16 to 60, with an average of 34—and comparing the average of their coefficients of mutual association with the general average coefficient for the entire group, with its 82 occurrences to the species. From Table V. it appears that this general coefficient for the seven least frequent species taken separately is 1.85, while that for the whole group of thirteen (Table I.) is 2.02—a coincidence probably as close as could be expected in view of the fact that the former number is an average of only 21 coefficients and the latter of 78. The coefficient expressing frequency of mutual association among these least frequent species, is thus so close to the general coefficient for the entire group that even the former species may be said to occur frequently enough in the collections for the purposes of this discussion.

RELATIONS TO PHYSICAL ENVIRONMENT.

I have next to study the interrelations of this group of darters by means of another and widely different set of data, to be derived from an analysis of collectors' records concerning the kinds of waters and the classes of situations from which the several collections came; and to compare the conclusions thus reached concerning the physical relations of the species with those already derived from an analysis of their relations of association. For this purpose these records have been organized in a way to show the relative frequency of the occurrence of each species in our collections in each of the three sections—northern, central, and southern Illinois, as the state is commonly divided; in each of the ten stream systems, or river basins, distinguished by us; and in each kind or class of body of water—whether stream, lake, pond, or marsh—the classification made expressing differences in size, in water movement, and in the character of the bottom.

EQUALIZATION OF THE DATA.

The data available are not equally numerous under these various heads. Those concerning the size and general character of water bodies, and the distribution by stream systems

and sections of the state, are inclusive of all our collections; but in many cases data are wanting definitely *descriptive* of the waters and the situations from which the collections were made. This is owing to the fact that the present use of these materials was not foreseen in the beginning of our collection period, nor, indeed, until the greater part of the field work had been done, and the records of the earlier years are consequently often incomplete for the present purpose. Later, collectors were instructed to make full descriptive notes, from the ecological standpoint, of each body of water visited and of each location at which a haul of the seine was made, and the whole body of the data of local distribution and ecological preference is such that if used with due discretion it may be expected to throw considerable light on the associative relationships of this little group of fishes.

These data have been worked out, in the same manner as in the preceding section of this paper, in the form of percentages of frequency of the occurrence of each species in each geographic or hydrographic subdivision and in each ecological situation. As the numbers of collections made have varied widely for the several areas and situations, those from one being often many times as numerous as those from another, it was necessary to reduce the frequency ratios of the several species in each area to a common standard for comparison. These numbers have been equalized, and confusing discrepancies removed, by reducing the collection data to percentages of the same base, which, for convenience, has been made one hundred collections.

DISCUSSION OF ECOLOGICAL TABLES.

If equal numbers of miscellaneous collections had been made from each situation, and if the total number of collections were such that any given darter had been taken one hundred times, what number or percentage of these collections of darters would have come, according to my present data, from each of the situations represented?

The figures in Table VI. are answers to this question; and

when I say that 63 per cent. of our collections of *Hadropterus phoxocephalus* are from rivers and 26 per cent. from creeks; or that 94 per cent. of them are from waters with a bottom of rock and sand and only six per cent. from mud; this means that if miscellaneous collections of fishes of all descriptions had been made from all kinds of Illinois waters until one hundred of them contained darters of this species, then sixty-three of the hundred would have come from rivers and twenty-six of them from creeks, ninety-four of them from rock and sand, and six of them from mud.

The ratios of this table differ in significance from those of my tables of associative coefficients in the fact that while the latter exhibit various degrees of *associative* relationship between species, the former express the tendencies or preferences of the species with respect to the features of the *physical* environment. An understanding of these physical relations of a species must help us to understand and explain its associative relations, and the one set of data may be expected to serve as a test of the completeness and correctness of the other.

THE DARTERS AS AN ECOLOGICAL GROUP.

It is well known that the darters as a group are most likely to be found in comparatively swift and rocky streams, and that they are especially adapted, by their small size, their large paired fins, their pointed heads, and their habit of resting on the bottom, for maintaining themselves in swift currents, and for securing from among and under stones the insect larvæ and crustaceans on which they mainly depend for food. This fact is clearly reflected in my Table VI., of "Local Preferences of Darters", from which it appears that 70 per cent. of our collections of the thirteen species were obtained from the smaller streams, 77 per cent. from swift waters, and 82 per cent. from waters with a bottom of rock and sand. Only 12 per cent., in fact, came from lakes and ponds, and 18 per cent. from waters with a muddy bottom.

THE TYPICAL AND THE NON-TYPICAL SPECIES.

A comparison, in respect to the strength of their local preferences, between the six species which, by means of an analy-

sis of their associative ratios, I have distinguished as typical and the six less typical species, shows that the more typical group occurs in the smaller rivers and creeks in 88 per cent. of these collections, and the less typical in 47 per cent.; the first group, in swift waters in 88 per cent. of the cases, and the second in 62 per cent.; the first, in rocky or sandy streams in 91 per cent., and the second in 66 per cent. That is, the frequency of occurrence of the less typical species in small rivers and creeks is 53 per cent. of that of the more typical species; in swift waters it is 71 per cent., and on rock and sandy bottoms it is 72 per cent.,—an average of 65 per cent. for these three factors. These purely ecological ratios agree in a significant manner with the corresponding averages to be drawn from the tables of associative frequencies, as may be seen by reference to Table I. If we average separately the totals for the first six and the last six species of that table, we find the average of the latter group to be 63 per cent. of that of the former—the difference in degree of associative affiliation is essentially the same as the difference of ecological relationship, the one conclusion confirming, and likewise explaining, the other.

It is further to be noticed, of the ecological affinity of the six selected species, that no one of them has been found in upland or glacial lakes; that their occurrence in lowland lakes, ponds, and sloughs—an average of only 1 per cent.—is so rare as to be negligible; and that, omitting *Ammocrypta pellucida*, which is in some respects peculiar, the frequency ratio for the larger rivers ranges from 3 to 9 per cent., with an average of only 5.5 per cent. for these species. This uniformity of their ecological relationships, which makes of them a well defined ecological group, is the explanation, of course, of their high degree of associative affiliation. The most notable specific differences among them are the relative frequency of *Ammocrypta pellucida*, and the absence of *Diplesion blennioides*, in my two hundred and ninety-three collections from the larger rivers.

The six less typical species, on the other hand, have little in common except their difference from this more typical group. *Boleosoma nigrum*, of which we have two hundred and

thirty-six collections, is an abundant and wide-ranging species, with comparatively feeble ecological preferences, as is shown by the fact that 15 per cent. of these collections are from lakes, 32 per cent. from still waters, and 11 per cent. from those with a muddy bottom. *Percina caprodes* (sixty collections) makes a similar showing, this being also a lake species in part (19 per cent.); but it differs from the preceding in the fact that it has occurred more frequently in the larger streams (10 per cent.), less frequently in still waters (7 per cent.), and not at all on muddy bottoms. *Cottogaster shumardi*, so far as may be judged from our sixteen lots of this species, is peculiar in its frequency in the larger rivers (55 per cent.) and the lowland lakes (18 per cent.), and in its avoidance of the smaller streams (only 4 per cent. in the creeks and smaller rivers). *Etheostoma jessie* (one hundred and fifty-eight collections) is an indifferent species, and occurs in almost equal ratios in large rivers, small rivers, creeks, and lowland lakes. *Boleichthys fusiformis*, which we have taken fifty-six times, is rare in the larger rivers, and seems to be the commonest of all our species in the upland lakes. *Boleosoma camurum* (one hundred and seven collections) is somewhat less indiscriminate in its local preferences. It is commonest in creeks (42 per cent.) and relatively rare in the larger rivers (9 per cent.). It apparently has no marked preference for swift waters over slow, nor for a hard bottom as compared with one of mud.

The ecological heterogeneity of these least typical species is reflected in their relatively feeble associative affiliations, these six species having a mutual associative ratio (derived from Table II.) of 1.4, while the corresponding ratio of the first six more typical species of Table II. is 3.28.

ASSOCIATION AND DISTRIBUTION.

The association of species may be looked upon as a consequence of their distribution. Species of wholly different general, or geographical, distribution can, of course, never be associated; and the same is true of those of wholly unlike local distribution. Those whose areas of general distribution merely

overlap, will be less frequently associated, other things being equal, than those whose distribution areas are identical; and species which are equally attracted to some local situations and unequally attracted to others, will be less frequently associated than those whose local preferences are altogether similar. Furthermore, if two species which occupy the same situations in the same area have a widely unlike abundance in different parts of this area—one being much the most abundant to the north, for example, and the other to the south—these species will occur together in collections less frequently, will have a lower coefficient of association, than if the two were most abundant in the same section and least abundant in the same. The number of joint occurrences will be conditioned, in part, in each section of the common area, by the abundance there of the less abundant species. It is impossible, consequently, to distinguish, by a simple inspection of a table of coefficients, local from general factors among the determining causes of difference in associative frequency. For this purpose maps of species distribution, and tables showing the locality preferences of species (like my Table VI.) must be studied in connection with tables of associative coefficients.

The causes controlling general distribution and local distribution are alike ecological, those affecting general distribution being usually general—climatic, topographic, hydrographic, and the like—and those affecting local distribution being local. In a small area like that of Illinois, one in which there are comparatively few physical barriers to the intermingling of fishes, these two classes of causes are not widely different, but they must nevertheless be distinguished, so far as possible, if we are to have a clear and correct knowledge of ecological relationships.

COMPARATIVE STUDY OF TABLES AND MAPS.

As an example of the manner in which these factors may be separated by a comparison of my tables and maps, and of the extent to which associate relationships may be accounted for, we may take a few instances of very low, and others of

very high, coefficients from Table II., and look up the facts concerning the species compared, as given in Table VI. and in the distribution maps appended to this paper. Thus far, it may be noticed, I have dealt with aggregates and average numbers only, which, owing to the heterogeneous and variable character of the data, are much more likely to be uniformly reliable than are the separate entries of the tables. The present discussion will, however, necessarily bring into comparison these separate entries, and the reasonableness and consistency of the conclusions reached by it may serve as some measure of the validity of their individual coefficients.

By reference to Table II. it will be seen that zeros appear at five points, in place of coefficients of association—an indication that representatives of the several pairs of species concerned have never been taken together by us in the same collection. This, as already pointed out, must mean either a complete difference in general distribution, so far as represented by my collections, or a very radical difference in locality preference.

Species 1443 and 1461 (*Diplesion blennioides* and *Etheostoma zonale*) are examples. A glance at the distribution maps of these species will show that each has been taken by us only in a different part of the state from the other, *blennioides* being confined to the Wabash valley, with the exception of a single collection at Chicago, and *zonale* being limited to the Illinois and Rock river systems. It seems difficult to believe that the flat and indefinite watershed separating the tributaries of the Wabash from those of the Illinois, can constitute a physical barrier sufficient to prevent the intermingling of these two species. On the other hand, it must be admitted that their ecological relations, as expressed in their preferences of situation, are, on the whole, very similar, as may be seen by a comparison of the two in Table VI.

A similar explanation is to be made in the case of *Diplesion blennioides* and *Cottogaster shumardi* (1443 and 1436). Here the areas of our collections of these two species are entirely separate, with the exception of a single collection of *Cottogaster* from the Wabash valley—to which *Diplesion* was entirely con-

fined. Furthermore, *Cottogaster* has been taken only in the larger streams or their immediate neighborhood, as is shown by the distribution map for that species; while *Diplesion* is limited to the smaller rivers and creeks.

With respect to *Cottogaster shumardi* and *Etheostoma cæruleum* (1436 and 1477), the case is a little less clear, and it is quite possible that with a larger number of collections containing the former species, the two might have been found in company. It is true that only 4 per cent. of our collections of *Etheostoma cæruleum* have come from the larger rivers and from stagnant waters to which *Cottogaster* is confined. On the other hand, a concurrence of the locality marks on the maps of distribution of these species (Maps V. and XII.) shows that the two were taken from the same locality—although not in the same collections—in three out of nine possible cases.

The lack of any coincident occurrence of *Cottogaster shumardi* and *Etheostoma zonale* (1436 and 1461) is explained by a glance at the maps (V. and X.), as due, not to a difference of geographical distribution, which is approximately identical for the two, but to that of local preference, the former species occurring only in or near the largest streams, and the latter being limited to the smaller rivers and creeks. Indeed, the two species were not taken by us from even the same locality at any time.

Nearly the same may be said of *Diplesion blennioides* and *Boleosoma camurum* (1443 and 1448), which have come from the same locality but once, although in general distribution they are not mutually exclusive. *Blennioides*, as may be seen from Table VI., is a species of more indefinite preferences than *camurum*, and occurs in various situations from which the latter is excluded.

I take up next five pairs of species, representatives of which have been occasionally taken together by us, but the coefficients of whose association are nevertheless very small.

Etheostoma zonale and *E. jessie* (1461 and 1474), for example, with an associative coefficient of only .37, show a pre-

ponderant abundance of the first in the north half of the state and of the second in central and southern Illinois. Among the twenty-nine localities from which the first of these species was taken, and the fifty-four for the second, there were but two in which both were found, and at each of these localities they occurred in only one collection. That is, in one hundred and eighty-eight separate collections of one or the other of these species from these various localities, the two were taken together but twice—a fact to be connected partly with the limitation of *Etheostoma zonale* to the northern half of the state, and partly with differences in the bodies of water in which these species habitually occur. Twenty-one per cent. of our collections of *jessie* came from the larger rivers, and only 3 per cent. of those of *zonale*; 19 per cent. of *jessie*, from the smaller rivers and creeks, and 74 per cent. of *zonale*; 24 per cent. of *jessie*, from lakes and ponds, and none of *zonale*.

Boleosoma camurum and *Etheostoma zonale* (1448 and 1461), whose coefficient of association is but .39, furnish an example of the relation of distribution already referred to, the area of the two species overlapping, but not coinciding throughout—that of *zonale* expanding to the northward and that of *camurum* to the southward. Partly in consequence of this fact, we have but a single joint occurrence of these species out of one hundred and thirty-eight collections containing one or the other. Their ecological relations, as shown by Table VI., are also quite unlike, *Boleosoma camurum* occurring in sluggish or stagnant waters five times as frequently as the other species, and in waters with a muddy bottom in a still greater differential ratio.

The low associative coefficient (.63) of *Hadropterus phoxcephalus* and *Boleichthys fusiformis* (1418 and 1494) is largely explained by the difference in preponderant distribution, the former being commonest in the Illinois valley and to the northward generally, while the latter is much the most abundant in the Wabash system and in extreme southern Illinois. In one hundred and thirty-eight collections containing one or the other of these species, they have occurred together but three times,—twice in branches of the Little Wabash River and

once in the Saline. The ecological relationships of the species are likewise very different, *phoxocephalus* showing a much stronger tendency than *fusiformis* to the larger streams. It occurs, for example, according to our data, in rivers in 63 per cent. of the cases, as against 13 per cent. for the other species. It also prefers swift to moderate water much more strongly, if I may judge from the small number of collections for which this factor was recorded, the ratios for swift water being 87 per cent. for *phoxocephalus* and 22 per cent. for *fusiformis*. A corresponding difference is seen in respect to the character of the bottom, 66 per cent. of our collections of *fusiformis* coming from waters with a muddy bottom and only 6 per cent. of those of *phoxocephalus*.

Boleosoma nigrum and *Etheostoma jessiae* (1446 and 1474), with their coefficient of .99, may serve as an example of species similarly distributed but essentially indifferent as associates, a coefficient of 1, it will be remembered, indicating a neutral relation. A glance at the distribution maps of the species shows at once some notable differences. *Boleosoma nigrum*, the most abundant of our darters, and taken by us in two hundred and thirty-six collections, has virtually the same geographical distribution as the other species, but it is represented in the larger rivers in very much smaller ratio. The marks of local distribution for the more abundant species are widely and rather uniformly scattered over the map, with but few on the larger streams, while those of the less abundant species are strung, like beads, along the principal rivers of the state. On the other hand, neither species is definitely excluded from either the territory or the situations of the other, as may be seen by a comparison of the figures for them given in Table VI.

Turning now to pairs of species with extraordinarily high associative coefficients, I may call attention first to *Etheostoma zonale* and *Etheostoma caeruleum* (1461 and 1477), whose coefficient reaches the remarkable figure of 8.38. The general distribution of these species is substantially the same, except that *Etheostoma caeruleum* has a greater development to the south. *Etheostoma zonale* is much less numerous than *caeruleum*, but

both species have been found most frequently in the eastern part of the state. A close comparison of the distribution maps shows that both have been taken from eighteen of the thirty *localities* in which the less abundant one was found; and they have been taken together in seventeen of the one hundred and five *collections* containing either or both.

A comparison of their local preferences indicates a close agreement in ecological relationship. Each of the species was found in the larger rivers in 3 per cent. of the collections; *zonale* in 97 per cent. of those from the smaller rivers and creeks, and *cæruleum* in 89 per cent.—the remainder of the latter coming from lowland lakes and ponds (1 per cent.) and from various miscellaneous sources. Eighty-nine per cent. of the collections of *zonale* and 83 per cent. of those of *cæruleum* were from streams of swift or moderate flow; 89 per cent. of *zonale* and 92 per cent. of *cæruleum*, from rock and sandy bottom. The only notable difference between these species is the preponderant disposition of *zonale* towards the smaller rivers rather than the streams classed as creeks.

The next highest coefficient (5.69) is that of *Hadropterus phoxocephalus* and *Etheostoma zonale* (1418 and 1461), which have occurred together sixteen times in my one hundred and one collections of one or the other. Both have been taken from seventeen of the thirty localities in which we have found *zonale*. The general distribution of the two differs but little, except that *zonale* is very much less abundant than *phoxocephalus*, and has been limited much more closely to the Illinois and Rock river basins. The ecological ratios for *zonale* and *phoxocephalus* respectively are,—larger rivers, 3 per cent. and 7 per cent.; smaller rivers, 74 per cent. and 56 per cent.; creeks, 23 per cent. and 26 per cent.; lakes and ponds, 0 and 3 per cent. The ratios of preference for rapid and slow waters respectively are still more closely approximate—89 per cent. of *zonale* and 87 per cent. of *phoxocephalus* from moderate or rapid currents. The preferences of the two species for rock and sandy bottom are similarly close—89 per cent. for *zonale* and 94 per cent. for *phoxocephalus*.

The next coefficient in order of size, that of *Hadropterus phoxocephalus* and *Ammocrypta pellucida* (1418 and 1450), is 4.95. These species are virtually identical in general distribution, *pellucida* being, however, comparatively scarce. The two species have been taken in ten of the seventeen localities in which *pellucida* was found, and have occurred conjointly eight times in the ninety-six collections containing one or the other. In general ecological relationship they are very closely similar, both occurring infrequently in the larger rivers, and in smaller rivers more frequently than in creeks. *Ammocrypta pellucida* has not been taken at all in lakes and ponds, and *phoxocephalus* only to the amount of 3 per cent. Both are rapid-water species, and strongly prefer streams flowing over rock and sand to those with muddy bottoms.

Hadropterus aspro and *Ammocrypta pellucida* (1421 and 1450), with a coefficient of 3.97 based on their twelve joint occurrences in one hundred and sixty-six collections, were taken from the same localities in ten cases of a possible seventeen. *Ammocrypta pellucida*, although much the less abundant, is distributed in general precisely like *aspro*, except that it does not show so marked a preference as does the latter species for the eastern part of the state. With respect to the character of the streams in which these species are most generally found, the ratios are unusually similar, *pellucida* occurring, however, according to our data, more commonly in the larger rivers, and *aspro* more frequently in creeks. Neither has been taken by us in lakes or ponds. The ratios of preference for waters with a clean bottom are 84 per cent. for each.

Percina caprodes and *Etheostoma zonale* (1417 and 1461) were taken together four times in the eighty-eight collections containing either or both. Their associative coefficient is 3.55. Their general distribution is different in the fact that *caprodes* is the more abundant in the central and southeastern parts of the state. They were collected from the same localities seven times out of a possible thirty. In ecological relationships they are only fairly similar. Both occur in the larger rivers, but

Percina caprodes in the larger percentage. This species was likewise frequently found in lakes and ponds, from which *zonale* was entirely absent. Their relations to slow and rapid waters seem essentially the same, but while all the collections of *caprodes* were taken from sand and rock, 11 per cent. of those of *zonale* came from a muddy bottom.

Indeed, we have, for the first time, in these last two species, a pair whose ecological records do not seem to correspond quite closely to their associative coefficients—a fact which might be due to a number of collections of these species too small to give a reliable average, or to the influence of ecological factors not covered by the classification of Table VI. *Percina caprodes* was represented by sixty collections, and *Etheostoma zonale* by thirty-two; but I have information concerning the relations of the species to the water current for only fourteen collections of the first species and eighteen of the second, and concerning their relation to the kind of bottom for only twenty of the first and nineteen of the second. On the other hand, it seems certain that the local distribution of darters must be affected by many things not referred to in Table VI.—variations in the mere instinct of segregation, in the kind of food preferred, in relations to the temperature and the chemical condition of the water, and the time of the year at which the greater part of the collections were made—involving, as this may, similarities and differences of the annual migratory movements of the species—and several other like conditions.

COLLECTIONS FOR ECOLOGICAL STUDY.

It has been the object of this paper to test the availability and the usefulness for ecological study, of the data of the careful zoological collector, by applying to them a special method of classification and analysis. At the same time, of course, the method itself has been severely tested; and it might have failed completely in this instance without being permanently discredited.

The unit of this paper is the collection; but this term as here used is highly various in its meaning, and to some extent

accidental in its denotation. It usually includes everything which it was convenient or desirable to catalog under one accessions number, with a mention of the date, place, and body of water from which the collection came, and, in the majority of cases, particulars concerning the apparatus used and the more notable features of the situation. It may cover at one time the product of a single haul of a small minnow seine from a rivulet or a pond, and at another time that of a number of longer hauls with a larger seine from a great lake or from a considerable stretch of the course of a great river; and in this discussion no account has been taken of differences of condition, season, or time of day, represented by the several accessions numbers.

If each collection had been made as much like every other as practicable in respect to the apparatus used, the proportionate area covered, and the definiteness and distinctness of the unit of environment from which it was drawn; if these ecological situations had been skilfully chosen, fully described, and thoroughly "sampled" as to the contents in fishes; and if collections, of moderate size but ample in number for the territory covered, had been judiciously repeated for each situation at different seasons and under varying conditions,—we should doubtless have obtained for our tables coefficients capable of yielding a larger and more complex knowledge than I have here presented of the local distribution of fishes under the influence of their environment.

In a later paper, in course of preparation, the writer intends to discuss, in a similar manner, the local and ecological relations of all the species obtained from a limited area—that of the Wabash valley in Illinois.

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EXPLANATION OF TABLES AND MAPS.

In place of the names of species, the corresponding numbers of Jordan and Evermann's "Synopsis of North American Fishes" have been used in the construction of the tables, as follows:—

- 1417. *Percina caprodes* (Raf.).
- 1418. *Hadropterus phoxocephalus* (Nelson).
- 1421. *Hadropterus aspro* (Cope & Jordan).
- 1436. *Cottogaster shumardi* (Gir.).
- 1443. *Diplesion blennioides* (Raf.).
- 1446. *Boleosoma nigrum* (Raf.).
- 1448. *Boleosoma camurum* Forbes.
- 1450. *Ammocrypta pellucida* (Baird).
- 1461. *Etheostoma zonale* (Cope).
- 1474. *Etheostoma jessie* (Jordan & Brayton).
- 1477. *Etheostoma caeruleum* Storer.
- 1490. *Etheostoma flabellare* Raf.
- 1494. *Boleichthys fusiformis* (Gir.).

Table I. shows, under each species number, first, the number of collections of the species used in this study; second, the coefficients of the association of the species with each of the others of the group of thirteen represented by this table, these coefficients being arranged in order of magnitude from above downward; and, third, the totals and the averages for each column. The species columns are arranged in the order of their average coefficients. At the bottom of the table is the sum of the totals for the species and the general average of their average coefficients, the last being the general associative coefficient for the entire group.

In Table II. the species numbers are placed in like order at the top and at the side of the table, and the coefficient of any two species will be found at the point of intersection of the column for one with the line for the other. The upper right half of this table is the reversed duplicate of the lower left half, inserted for convenience in following a series of coefficients.

Table III. is constructed like Table II., but with totals and averages added, as in Table I. It contains the coefficients of mutual association of the last three species of Table I., which are distinguished by the lowest average coefficients of the whole series of thirteen.

Table IV. is constructed like Table III. It contains the coefficients of mutual association of the "typical darters"—the first six of Table I. distinguished by their high average coefficients.

Table V. contains the coefficients of mutual association of the seven species which have occurred least frequently in my collections.

Table VI. is intended to represent the relations of preference and avoidance of the various species with reference to kinds of bodies of water, to current movements, and to character of bottom, so far as these are determinable from our data. Where the ratios do not amount to 100 per cent., the difference is due to the omission of miscellaneous minor data.

The general map of the distribution of collections (Map I.) shows, by the location of the red spots, all the localities from which collections of fishes have been made by us in the work of the Natural History Survey. The distribution maps for the various species indicate in the same way all the localities from which representatives of the species have been taken. *For an accurate idea of the significance of these species maps, each should be compared with Map I.*

The following numbered list of the counties of the state corresponds to the numbers on these maps.

- | | | |
|------------------|-----------------|-----------------|
| 1. Jo Daviess. | 35. Hancock. | 69. Madison. |
| 2. Stephenson. | 36. McDonough. | 70. Bond. |
| 3. Winnebago. | 37. Fulton. | 71. Fayette. |
| 4. Boone. | 38. Mason. | 72. Effingham. |
| 5. McHenry. | 39. Tazewell. | 73. Jasper. |
| 6. Lake. | 40. McLean. | 74. Crawford. |
| 7. Cook. | 41. Vermilion. | 75. Lawrence. |
| 8. Du Page. | 42. Champaign. | 76. Richland. |
| 9. Kane. | 43. Piatt. | 77. Clay. |
| 10. DeKalb. | 44. Dewitt. | 78. Marion. |
| 11. Ogle. | 45. Logan. | 79. Clinton. |
| 12. Lee. | 46. Menard. | 80. St. Clair. |
| 13. Carroll. | 47. Cass. | 81. Monroe. |
| 14. Whiteside. | 48. Schuyler. | 82. Randolph. |
| 15. Rock Island. | 49. Brown. | 83. Washington. |
| 16. Mercer. | 50. Adams. | 84. Perry. |
| 17. Henry. | 51. Pike. | 85. Jefferson. |
| 18. Bureau. | 52. Scott. | 86. Wayne. |
| 19. Putnam. | 53. Morgan. | 87. Edwards. |
| 20. La Salle. | 54. Sangamon. | 88. Wabash. |
| 21. Kendall. | 55. Christian. | 89. White. |
| 22. Grundy. | 56. Macon. | 90. Hamilton. |
| 23. Will. | 57. Moultrie. | 91. Franklin. |
| 24. Kankakee. | 58. Douglas. | 92. Jackson. |
| 25. Iroquois. | 59. Edgar. | 93. Williamson. |
| 26. Ford. | 60. Clark. | 94. Saline. |
| 27. Livingston. | 61. Coles. | 95. Gallatin. |
| 28. Marshall. | 62. Cumberland. | 96. Hardin. |
| 29. Woodford. | 63. Shelby. | 97. Pope. |
| 30. Stark. | 64. Montgomery. | 98. Johnson. |
| 31. Peoria. | 65. Macoupin. | 99. Union. |
| 32. Knox. | 66. Greene. | 100. Alexander. |
| 33. Warren. | 67. Calhoun. | 101. Pulaski. |
| 34. Henderson. | 68. Jersey. | 102. Massac. |

TABLE I.—ASSOCIATIVE COEFFICIENTS OF THIRTEEN SPECIES OF DARTERS (ETHEOSTOMINÆ).

In order of size.

Species Numbers	1418	1461	1490	1421	1450	1477	1417	1446	1436	1443	1474	1448	1494
Collections	85	32	30	159	19	90	60	236	16	24	158	107	56
	5.69	8.38	4.44	3.97	4.51	8.38	3.55	3.25	4.17	3.48	2.77	3.34	3.34
	4.95	5.69	4.17	3.97	3.97	4.44	3.33	3.20	3.28	2.57	2.76	2.34	1.80
	3.33	3.97	3.80	3.20	3.28	2.73	3.13	2.90	3.13	2.45	1.89	1.89	1.57
	2.96	3.80	3.48	2.96	2.90	2.45	2.63	2.62	2.94	2.36	1.84	1.87	1.56
	2.94	3.55	3.25	2.73	2.63	2.36	2.45	2.45	2.77	2.14	1.69	1.32	1.52
	2.76	2.62	2.73	2.73	2.34	2.34	2.20	2.14	2.34	1.84	1.33	1.29	1.12
	2.57	1.56	1.80	2.20	2.14	1.83	1.87	1.69	1.57	1.77	1.27	.91	.99
	2.14	1.39	1.75	1.77	1.75	1.30	1.69	1.63	1.12	1.63	1.27	.62	.94
	1.83	.39	1.27	1.57	1.39	.99	1.69	1.52	.79	.24	.99	.50	.68
	1.32	.37	1.17	1.57	1.33	.77	1.30	.99	0.0	0.0	.77	.39	.63
	1.17	0.0	1.11	1.29	.94	.31	1.11	.91	0.0	0.0	.68	.31	.30
	.63	0.0	.62	1.27	.50	0.0	.30	.79	0.0	0.0	.37	0.0	.24
Totals	32.29	31.72	29.59	29.23	28.12	27.90	25.25	24.07	22.11	18.48	17.63	14.78	14.69
Averages	2.69	2.64	2.46	2.44	2.34	2.32	2.10	2.01	1.84	1.54	1.47	1.23	1.22
Probable Errors	±.28	±.43	±.25	±.18	±.24	±.26	±.15	±.16	±.20	±.16	±.14	±.16	±.16
Ratio of Prob. Errors to Averages	.104	.163	.101	.074	.103	.11	.071	.08	.109	.104	.097	.13	.131

Grand Total, 315.81. General Average, 2.02. (±.09)

TABLE II.—ASSOCIATIVE COEFFICIENTS OF THIRTEEN SPECIES OF DARTERS (EPHEOSTOMINÆ).
 In the order of the size of the coefficients of association of each species with *Hadiropterus aspro* (1421).

Sp.	Collections	Coefficients of association												
		1421	1450	1461	1446	1418	1490	1477	1417	1443	1436	1494	1448	1474
1421	159		3.97	3.97	3.20	2.96	2.73	2.73	2.20	1.77	1.57	1.29	1.29	1.27
1450	19	3.97		1.39	2.90	4.95	2.34	2.63	2.14	2.34	1.57	1.57	1.57	1.57
1461	32	3.97	1.39		2.62	5.69	8.38	3.55	0.0	0.0	1.56	1.39	1.39	1.39
1446	236	3.20	2.90	2.62		2.14	2.45	1.63	1.63	0.79	1.52	0.91	0.91	0.91
1418	85	2.96	4.95	5.69	2.14		1.83	2.57	2.57	2.94	1.80	1.32	1.32	1.32
1490	30	2.73	1.75	3.80	3.25	1.17		1.11	3.48	4.17	1.80	1.62	1.62	1.62
1477	90	2.73	2.34	8.38	2.45	4.44	4.44	1.30	2.36	0.0	0.99	0.31	0.31	0.31
1417	60	2.20	2.63	3.55	1.69	4.44	1.30							
1443	24	1.77	2.14	0.0	1.63	3.33	2.36	2.45						
1436	16	1.57	3.28	0.0	0.79	4.17	3.13	0.0	0.0					
1494	56	1.57	.94	1.56	1.52	1.80	.99	3.0	0.24	1.12	3.34	3.34	3.34	3.34
1448	107	1.29	.50	.39	.91	1.32	.31	1.87	0.0	2.34	.68	1.89	1.89	1.89
1474	158	1.27	1.33	.37	.99	1.27	.77	1.69	1.84	2.77	.68	1.89	1.89	1.89

TABLE III.— COEFFICIENT TABLE OF THE FOUR LEAST FREQUENT ASSOCIATES.

Species	1443	1448	1474	1494
1443		0.0	1.84	.24
1448	0.0		1.89	3.34
1474	1.84	1.89		.68
1494	.24	3.34	.68	
Totals	2.08	5.23	4.41	4.26

General Average, 1.33

TABLE IV.— COEFFICIENT TABLE OF THE SIX MOST FREQUENT ASSOCIATES.

Species	1418	1461	1490	1421	1450	1477
1418		5.69	1.17	2.96	4.95	1.83
1461	5.69		3.80	3.97	1.39	8.38
1490	1.17	3.80		2.73	1.75	4.44
1421	2.96	3.97	2.73		3.97	2.73
1450	4.95	1.39	1.75	3.97		2.34
1477	1.83	8.38	4.44	2.73	2.34	
Totals	16.60	23.23	13.89	16.36	14.40	19.72

General Average, 3.47.

TABLE V.— COEFFICIENT TABLE OF THE SEVEN LEAST FREQUENT DARTERS.

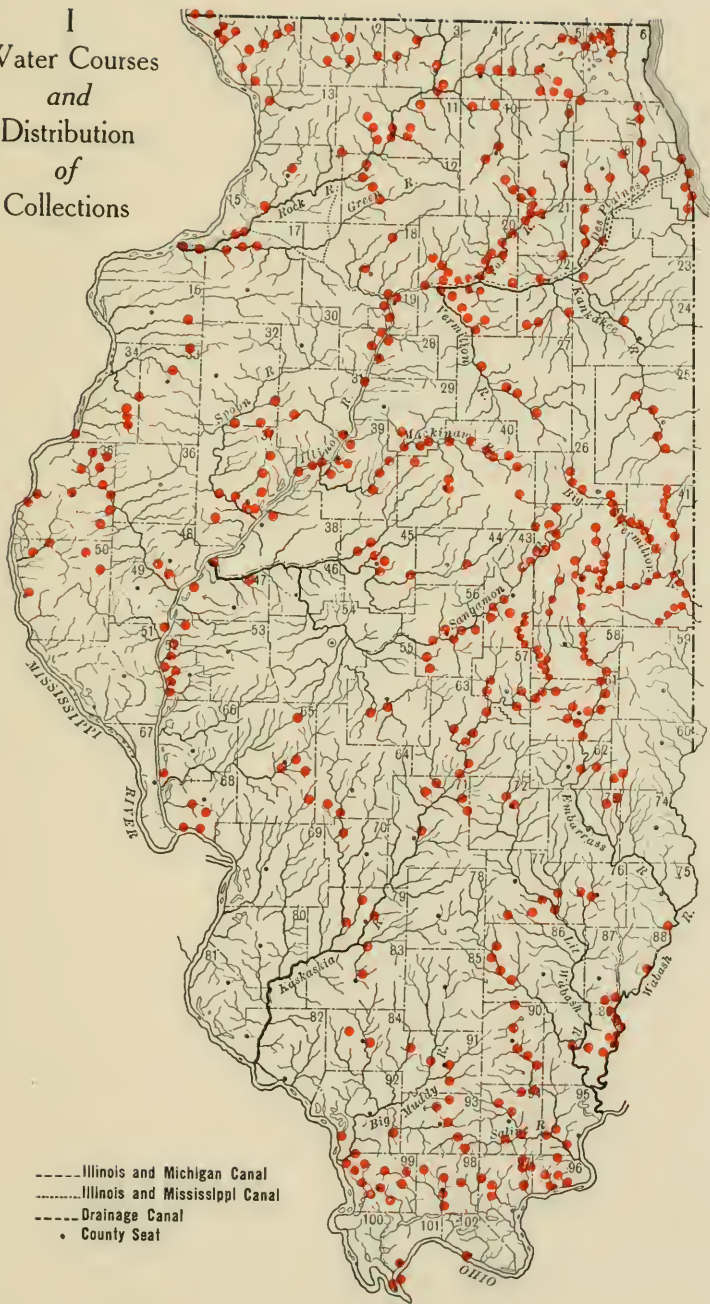
Species	1436	1450	1443	1490	1461	1494	1417
Collections	16	19	24	30	32	56	60
1436		3.28	0.0	4.17	0.0	1.12	3.13
1450	3.28		2.14	1.75	1.39	.94	2.63
1443	0.0	2.14		3.48	0.0	.24	2.45
1490	4.17	1.75	3.48		3.80	1.80	1.11
1461	0.0	1.39	0.0	3.80		1.56	3.55
1494	1.12	.94	.24	1.80	1.56		.30
1417	3.13	2.63	2.45	1.11	3.55	.30	
Totals	11.70	12.13	8.31	16.11	10.30	5.96	13.17

General Average, 1.85.

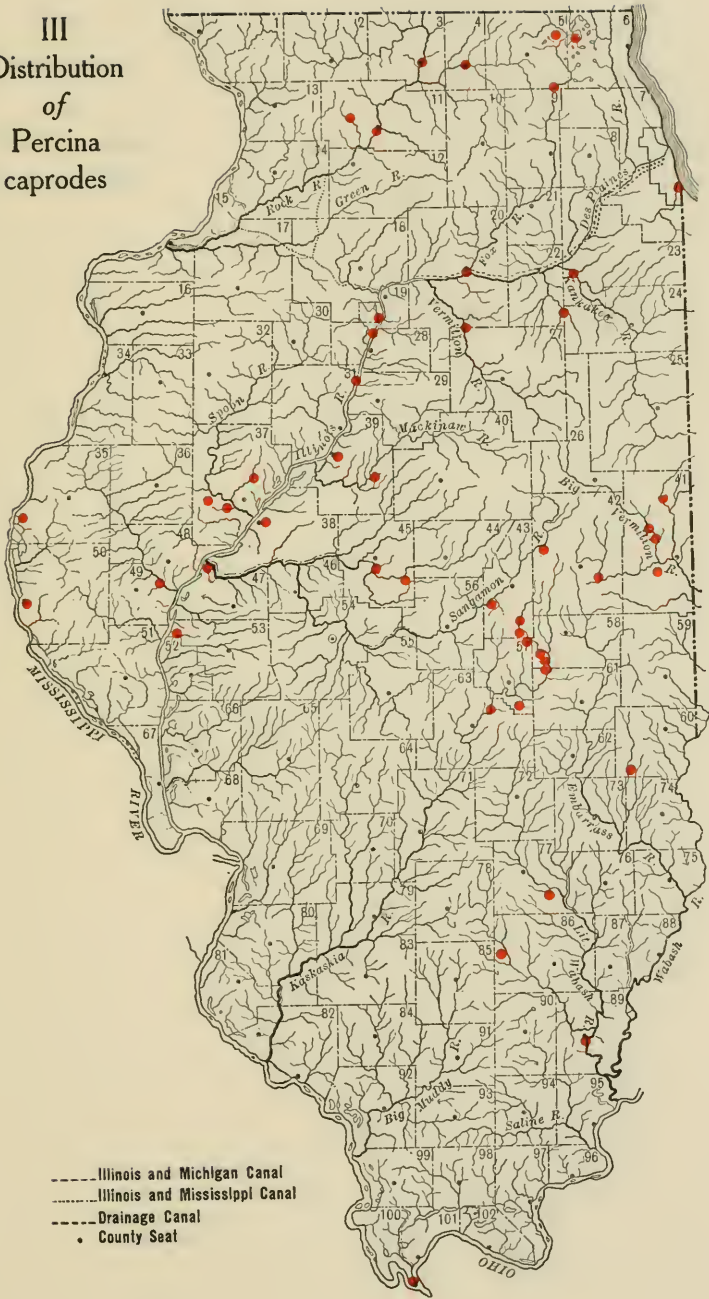
TABLE VI.—LOCAL PREFERENCES OF DARTERS.

Situations	1450	1443	1490	1418	1421	1461	1477	1446	1417	1436	1474	1494	1448	Av.
Larger rivers	.14	.00	.09	.07	.06	.03	.03	.03	.10	.55	.21	.01	.09	.11
Smaller rivers	.47	.47	.00	.56	.42	.74	.44	.25	.37	.00	.19	.12	.23	.33
Creeks	.39	.53	.87	.26	.47	.23	.45	.33	.27	.04	.16	.25	.42	.37
Lowland lakes, ponds, sloughs, etc.	.00	.00	.04	.03	.01	.00	.01	.01	.10	.18	.24	.02	.17	.06
Upland lakes, ponds, etc.	.00	.00	.00	.00	.00	.00	.00	.14	.09	.00	.00	.60	.00	.06
Moderate to rapid current	1.00	.83	1.00	.87	.69	.89	.83	.68	.93		.83	.22	.44	.77
Sluggish to stagnant	.00	.17	.00	.13	.31	.11	.17	.32	.07		.17	.78	.56	.23
Muddy bottom	.16	.00	.00	.06	.16	.11	.08	.11	.00		.23	.66	.62	.18
Rocky and sandy bottom	.84	1.00	1.00	.94	.84	.89	.92	.89	1.00		.77	.34	.38	.82

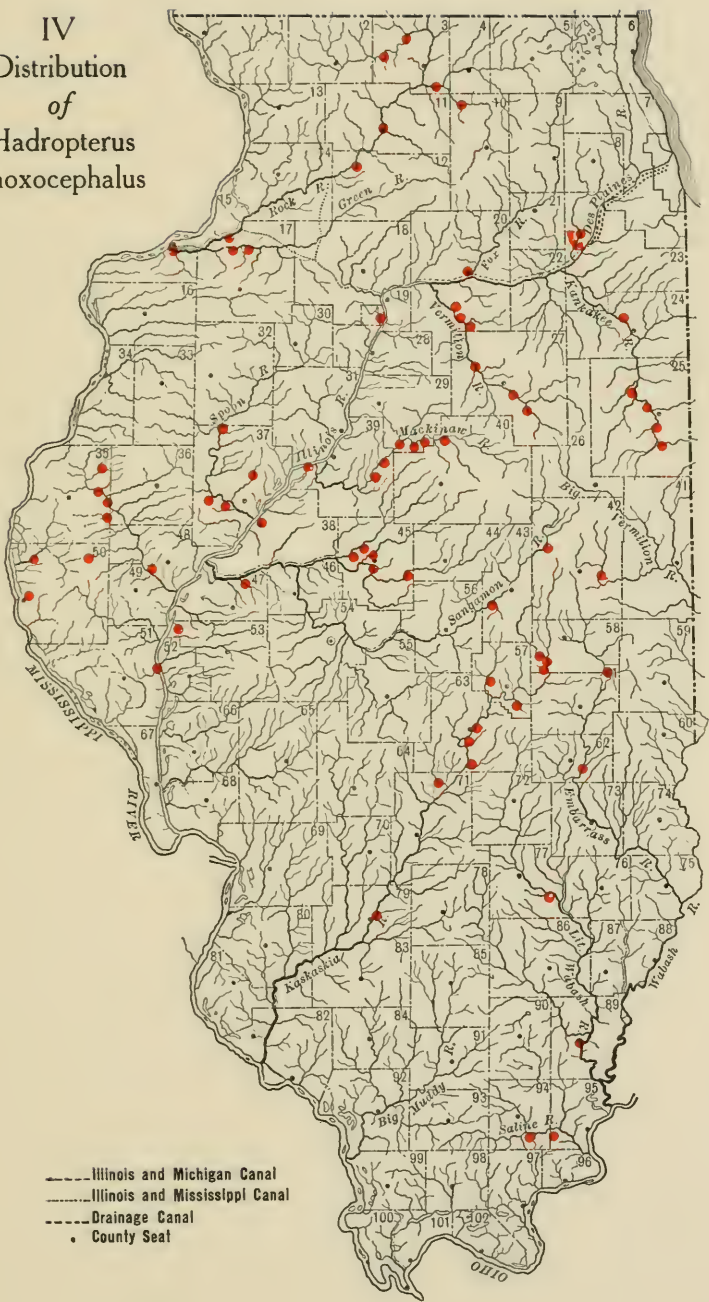
I
 Water Courses
 and
 Distribution
 of
 Collections



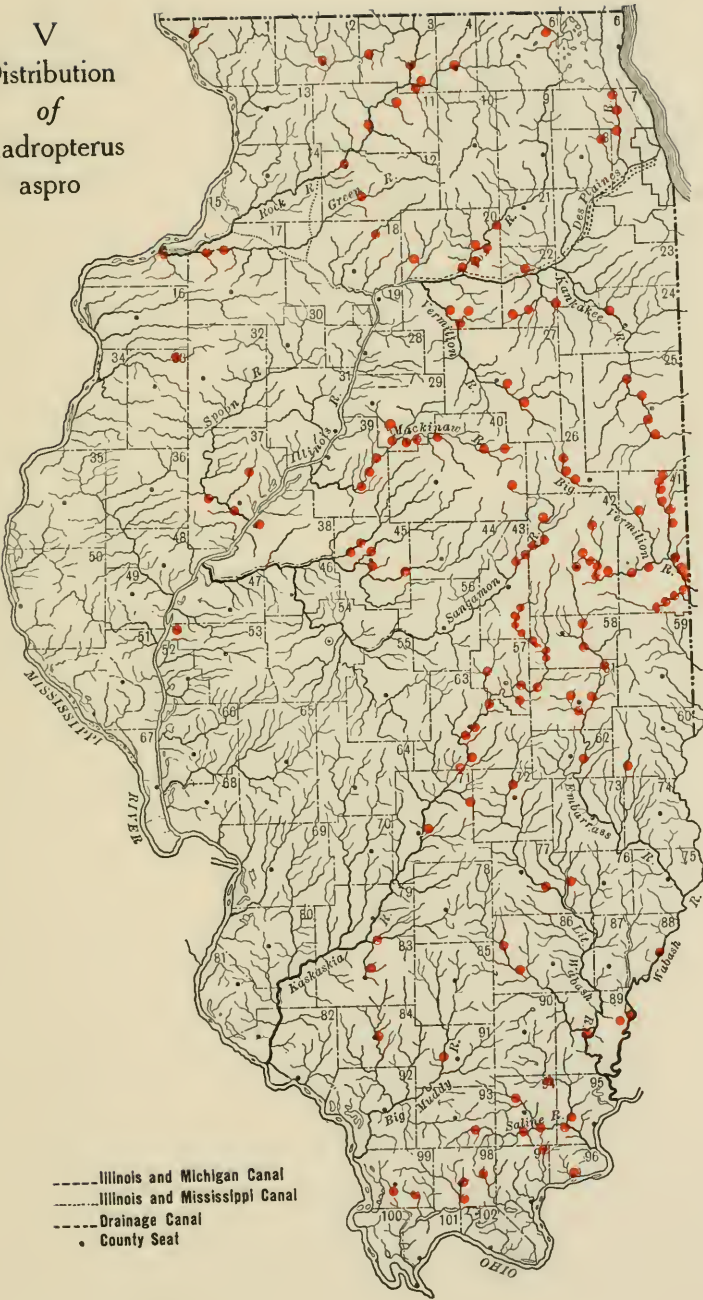
III
 Distribution
 of
Percina
caprodes



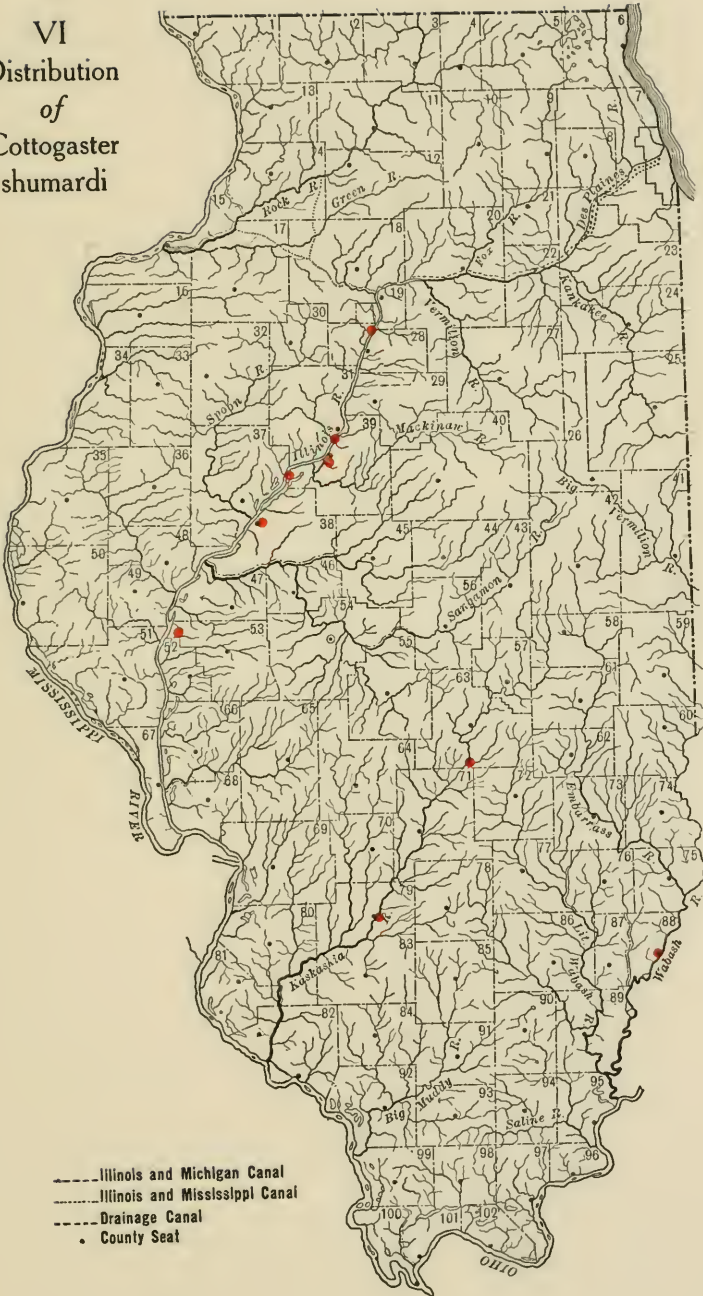
IV
 Distribution
 of
*Hadropterus
 phoxocephalus*



V
 Distribution
 of
Hadropterus
aspro



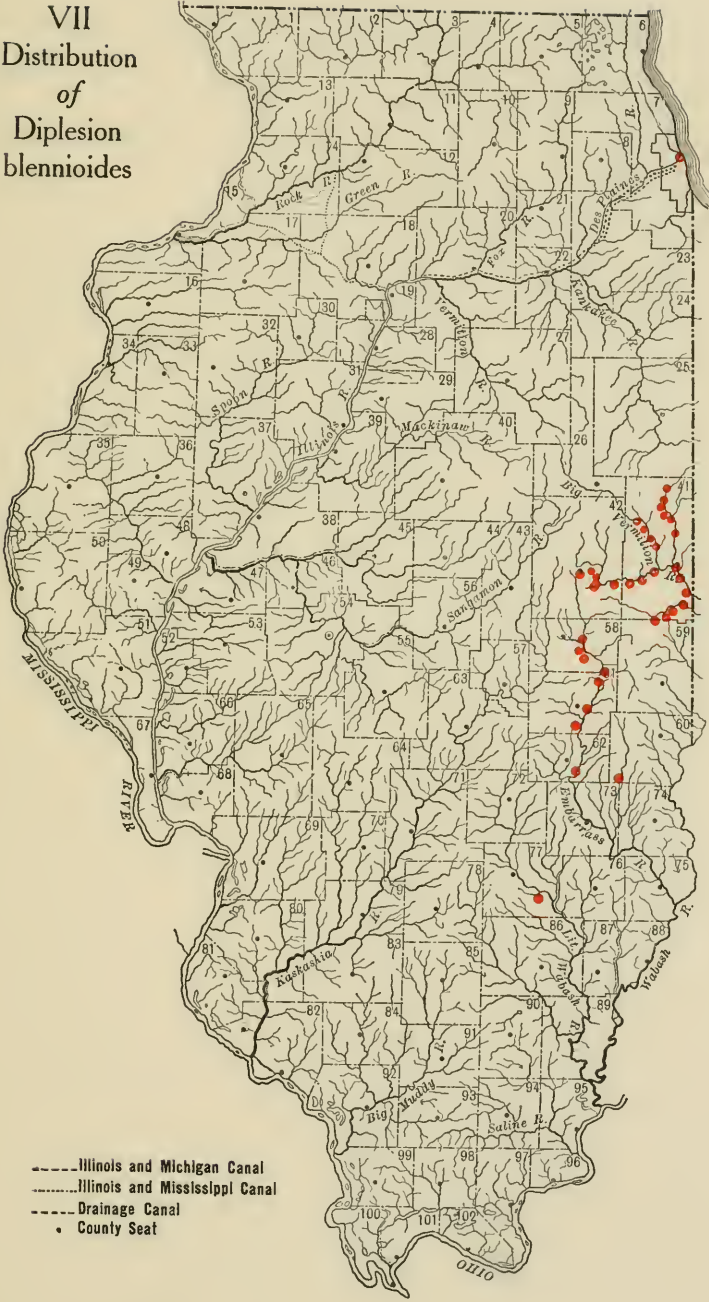
VI
 Distribution
 of
Cottogaster
shumardi



VI
Distribution
of
Cottonwood
Stems

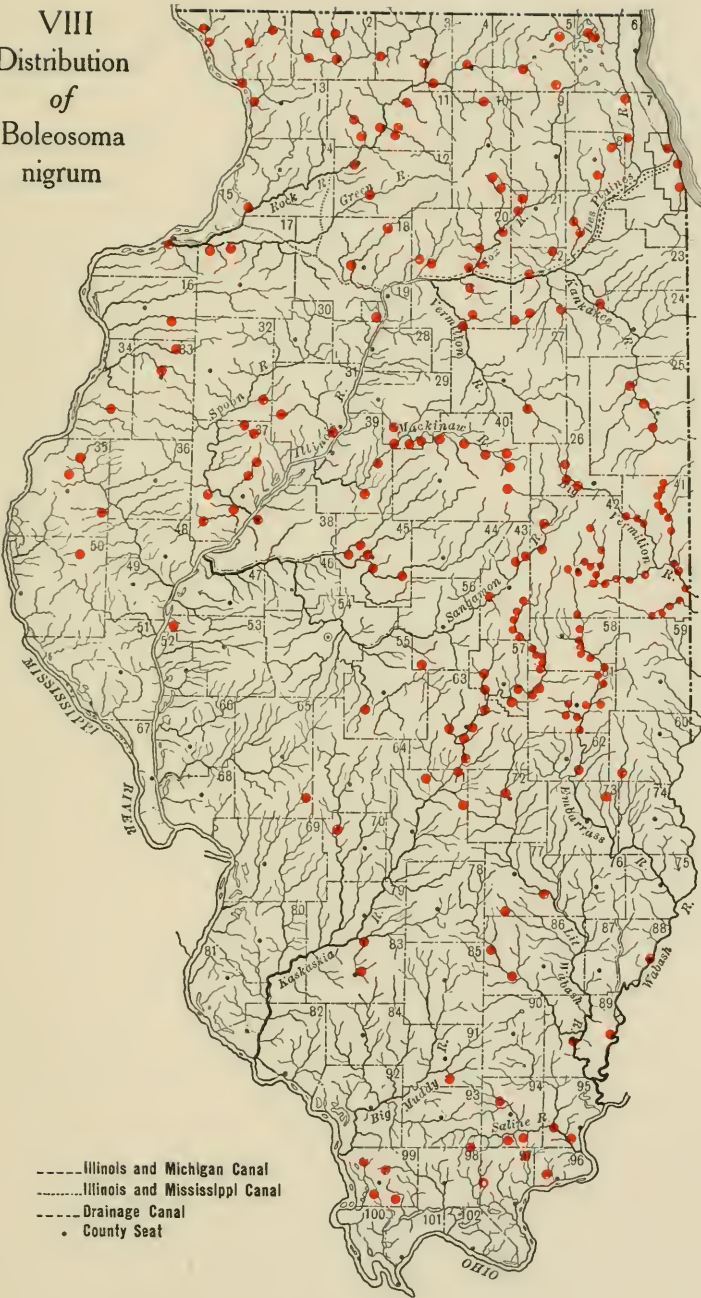


VII
 Distribution
 of
*Diplesion
 blennioides*

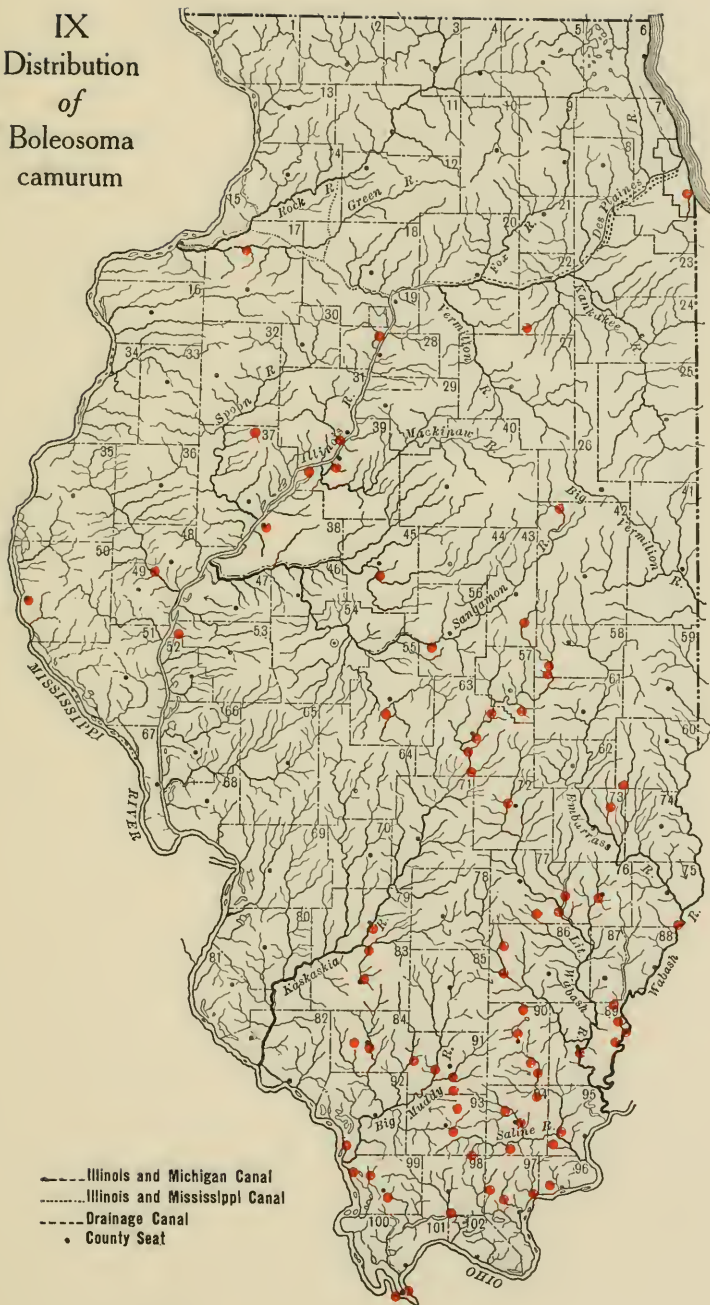


- Illinois and Michigan Canal
- Illinois and Mississippi Canal
- Drainage Canal
- County Seat

VIII
 Distribution
 of
Boleosoma
nigrum

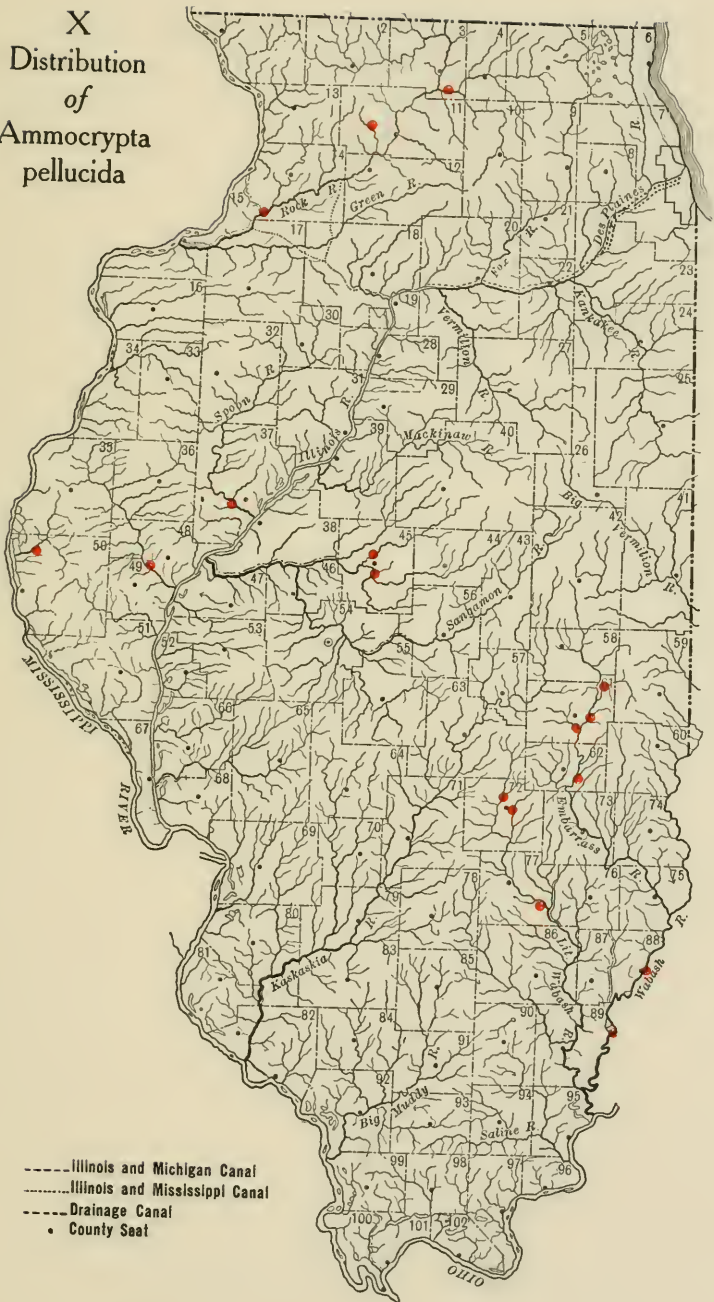


IX
 Distribution
 of
Boleosoma
camurum



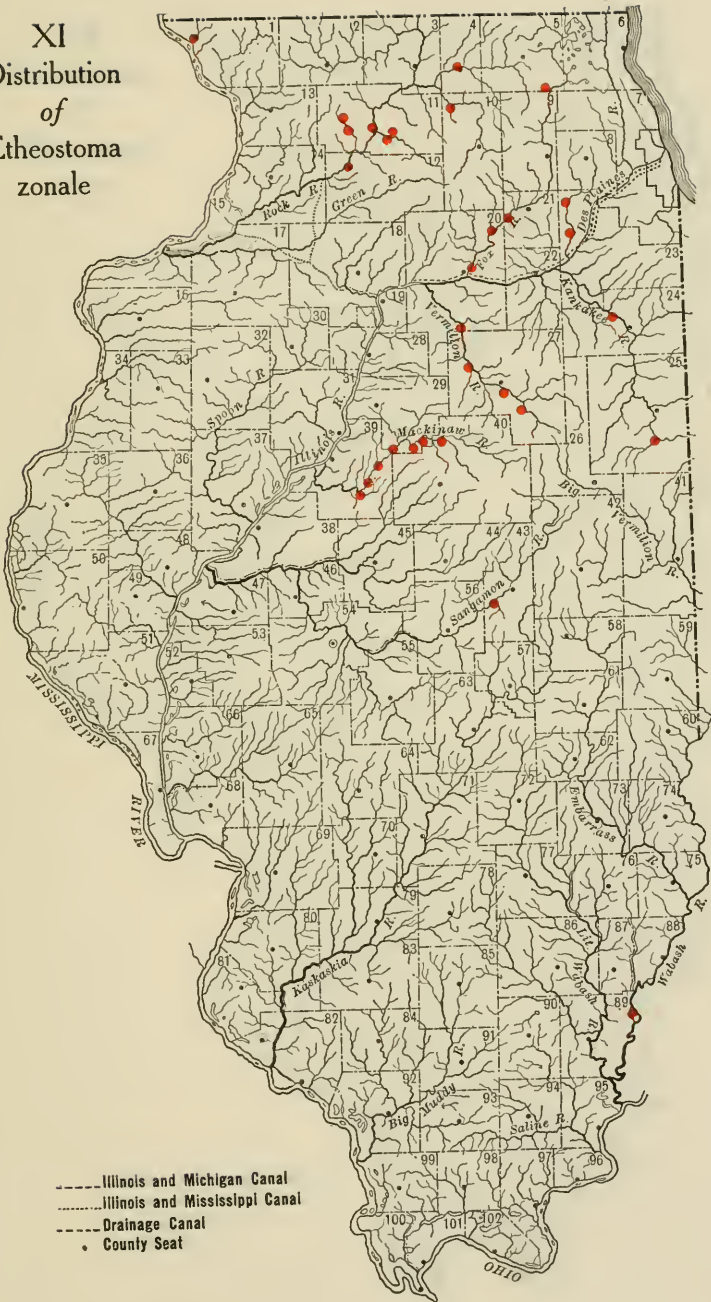
- Illinois and Michigan Canal
- Illinois and Mississippi Canal
- Drainage Canal
- County Seat

X
 Distribution
 of
*Ammocrypta
 pellucida*

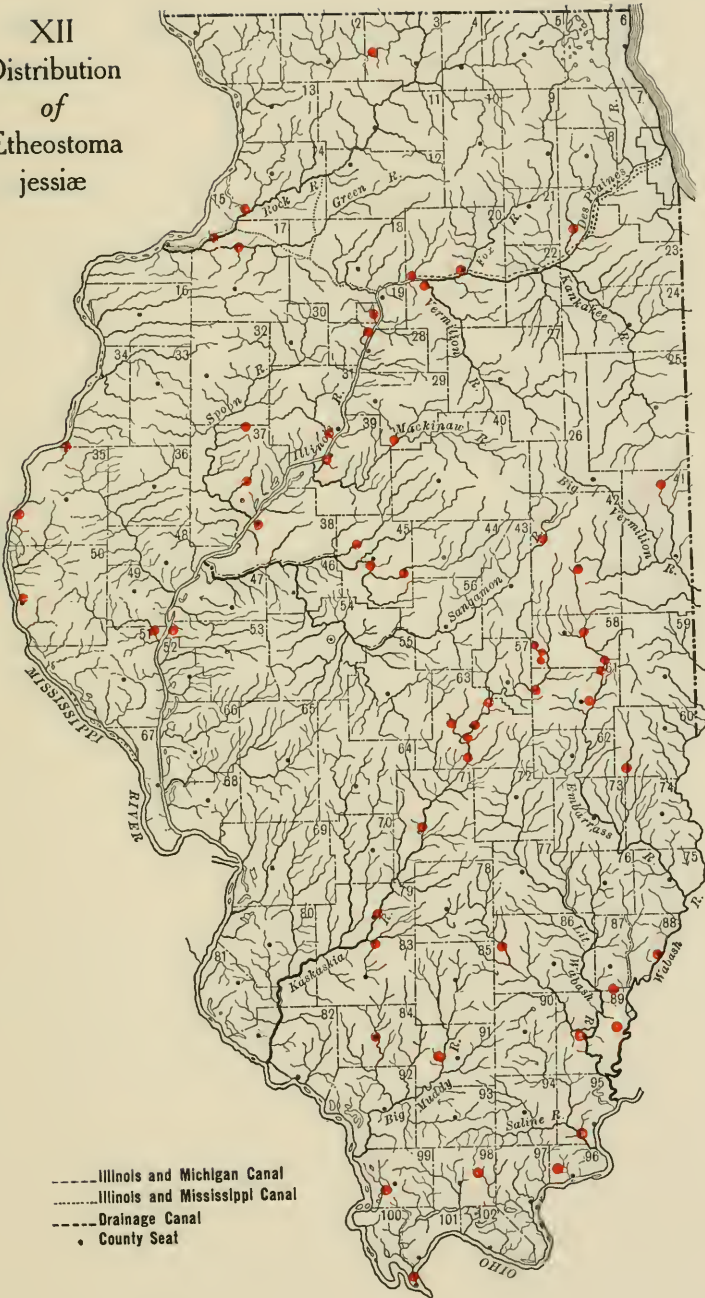


- Illinois and Michigan Canal
- Illinois and Mississippi Canal
- Drainage Canal
- County Seat

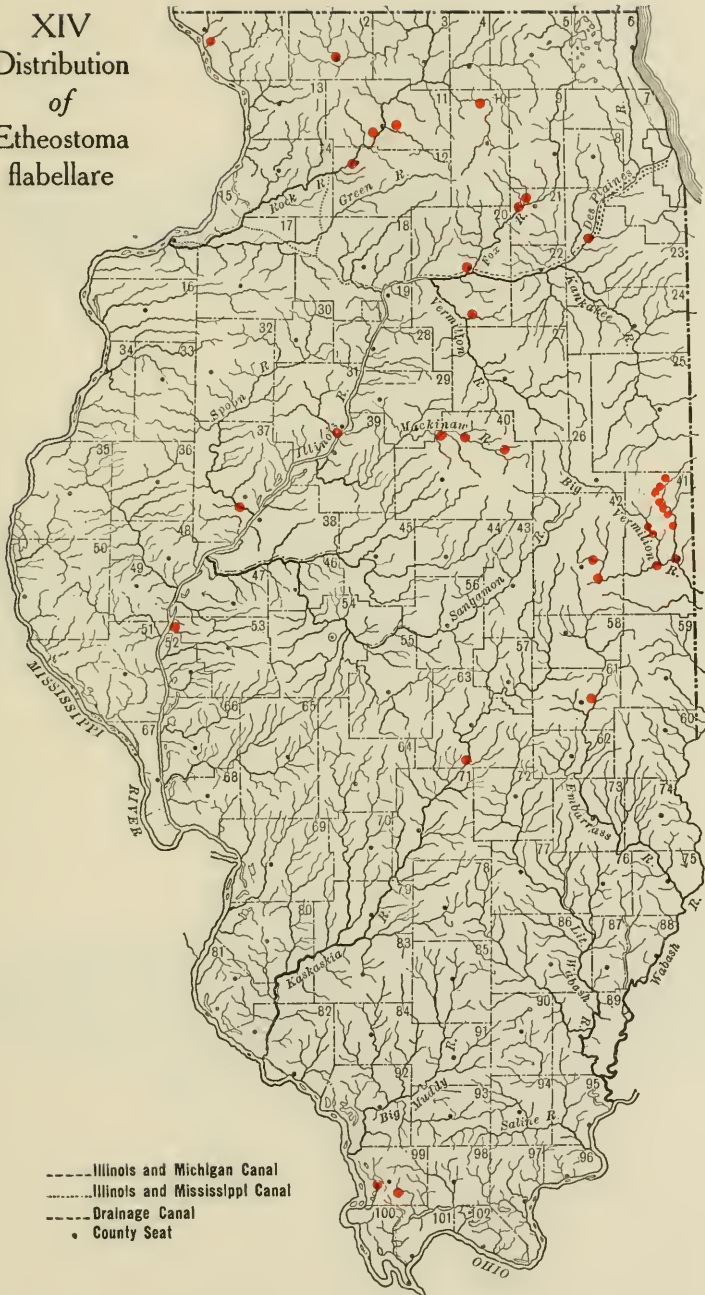
XI
 Distribution
 of
Etheostoma
 zonale



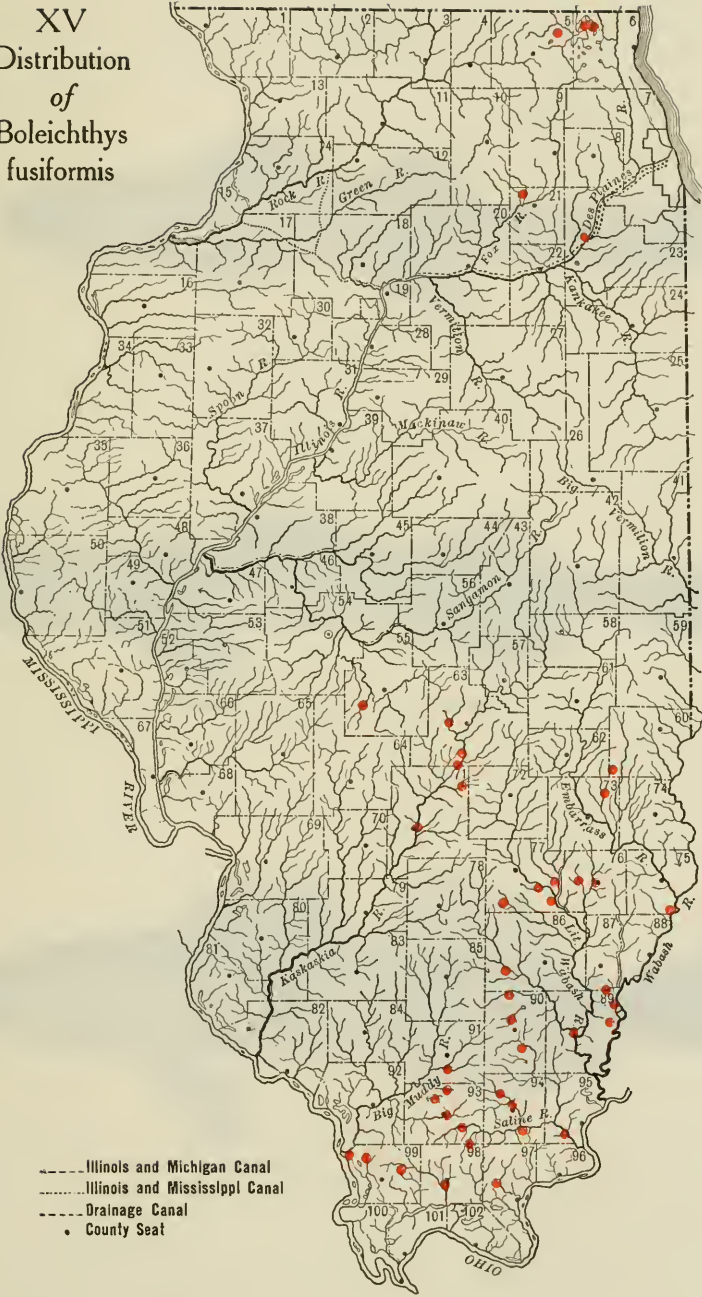
XII
 Distribution
 of
Etheostoma
jessiae



XIV
 Distribution
 of
Etheostoma
flabellare



XV
 Distribution
 of
*Boleichthys
 fusiformis*



XXIV.



Boleosoma camurum Forbes. x2.



SAND DARTER. *Ammocrypta pellucida* (Baird). x1 $\frac{2}{3}$.

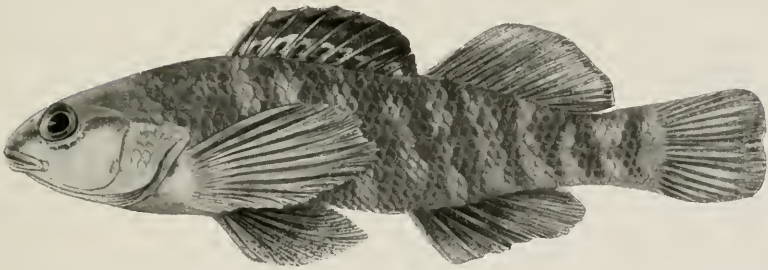


Cottogaster shumardi (Girard). x1 $\frac{3}{4}$.

XXV.



Boleichthys fusiformis (Girard). x2.



RAINBOW DARTER. *Etheostoma ceruleum* Storer. Male. x1¼



BANDED DARTER. *Etheostoma zonale* (Cope). Male. x1¼

XXVI.



GIANT DARTER. *Percina caprodes* (Rafinesque). X $\frac{3}{4}$.

XXVII.

NELSON'S DARTER, *Hadroterus phoxocephalus* (Nelson). X1½.



XXVIII.

BLACK-SIDED DARTER. *Hadiroterus aspro* (Cope & Jordan). X 1/4.



XXIX.



GREEN-SIDED DARTER. *Diplostion biennioides* (Rafinesque). Natural size.

XXX.



JOHNNY DARTER, Male. *Boleosoma nigrum* (Rafinesque). X13/4.

XXXI.

Etheostoma jessiae (Jordan & Brayton). X2.



XXXII.

FAN-TAILED DARTER. *Etheostoma flabellare* Rafinesque. XI 1/2.

