Summary.—In four tetraploid ($n = 36$) varieties of cultivated *Gaillardia aristata* the last premeiotic mitosis is shown to be similar to any other mitosis, each anaphase and telophase chromosome containing two chromonemata spiraled in the same direction and about each other. The last division before meiosis is located by finding delayed somatic mitoses in sporogenous tissue of an anther sac which is constantly four-rowed and almost invariably 30 to 35 cells in length. By tracing the chromonemata from the prophases of the last premeiotic mitosis to the heterotypic metaphases it is concluded that each thread in the premeiotic resting nucleus represents two chromonemata closely appressed and that the coiling relationships of the last premeiotic division persist through to the heterotypic prophases. Evidence was obtained from the direction of the chromonematal coils near chiasmata that chiasmata must be formed according to the one-plane theory.

[2] Kaufmann, B. P., *Bot. Rev.*, **2**, 529–553 (1936).
[3] Huskins, C. L., *Nature*, **132**, 62–63 (1933).
[4] Darlington, C. D., *Recent Advances in Cytology.* New York (1932).
[5] Cooper, D. C., and Mahony, K. L., *Amer. Jour. Bot.*, **22**, 843–848 (1935).
[6] Sax, K., *Genetics*, **21**, 324–338 (1936).

AN EVOLUTIONARY ANALYSIS OF INSULAR AND CONTINENTAL SPECIES

By Alfred C. Kinsey

Department of Zoölogy, Indiana University[1]

Discussions of evolutionary problems usually fail to take into account the varying constitution and behavior of species among different groups of plants and animals. The species problem becomes a number of problems if there are a number of different entities that pass as species. Quite aside from confusions introduced by differing concepts and definitions of the basic taxonomic unit, the qualities of inter-breeding populations among such diverse things as, for instance, strong-flying birds, parasitic insects, world-circling primates, microscopic fungi, bacteria, slow-fruiting angiosperms, and crustacea of the ocean plankton are so various that no single, simple explanation, or any theoretic ideal, can account for the evolution of all of them.

The relatively few forms which have been subjected by the geneticists to laboratory studies do not reflect the diversity which exists in nature; and

any extensive application of the laboratory data on evolution must await exhaustive taxonomic analyses of a variety of organisms. Until then evolutionary theorists can hardly know what conditions the theories must cover. In studies on the gall wasp family Cynipidae I have attempted to make such an application of the laboratory genetics. Experimental breeding is hardly possible with these insects because of their relatively long life cycles, peculiar life histories which involve an alternation of generations, and strict relations to particular plant hosts; but these very qualities are the sources of unusually significant material for taxonomic analyses of certain evolutionary phenomena.

On the immediate question of insular and continental species I can summarize data from the study of nearly 400 species of gall wasps belonging to the genera *Neuroterus, Cynips, Disholcaspis, Xystoteras* and some other smaller groups. The 75,000 miles of field work have been spread throughout the United States, Mexico and Guatemala in order that the analyses might cover all of the available species of the complexes and genera involved.

The opportunity to analyze insular species among these insects depends on the fact that each gall wasp is restricted to a single kind of oak or to a limited number of related oaks as hosts. Among the more than 300,000 individuals handled to date only 10 (i.e., 0.003%) have occurred on anything else than their normal hosts. Further isolation is also provided by the limitation of the oak hosts throughout most of the western United States, Mexico and Central America to high mountain elevations which stand like so many oceanic islands in a sea of deserts and tropic lowlands. For many groups of plants and animals the desert mountain ranges of our Southwest and Mexico offer better opportunities for the study of isolation than that afforded by any group of oceanic islands.

Practically all of the Cynipidae studied to date are classifiable as insular or continental forms. Only a few of the wider ranging species occurring in continuous mountain areas are not classifiable as one or the other of these types. Some 76% of the gall wasps studied are insular. Similar analyses of some other groups for which there are adequate taxonomic data show 74% insular species among the salamanders of the family Plethodontidae (Dunn 1926), 62% among the cave crickets of the genus Ceuthophilus (Hubbell 1936), possibly 15% among the pondweeds of the genus Potamogeton (Fernald 1932) and only 9% among the spiderworts of the genus Tradescantia (Anderson and Woodson 1935). Outside of oceanic island forms, there are few insular species among most groups of birds or mammals. Thus the number of insular forms varies widely in different groups, and the Cynipidae undoubtedly represent an extreme case but one that is matched among other forms more often than is usually recognized.

Most of the insular Cynipidae are located in the western half of the United States, Mexico and Central America; all of the continental species are found in the eastern half of this country and in Europe. In the western American and Mexican mountain areas the diversities of the topography directly effect the isolation of the insects, and indirectly limit them by isolating the species of oaks on which they occur. The only insular species in the eastern half of the United States and in Europe are those that are isolated by their hosts; but the oak species usually range so widely in these areas that most of the Cynipidae on them are continental in nature.

The ranges of the insular species are on a whole very much smaller than those of continental forms. The record is as follows:

	RANGES IN SQUARE MILES		
	MINIMUM	MAXIMUM	AVERAGE
225 Insular species	100	50,000	4,600
64 Continental species	10,000	1,500,000	300,000

For a third of the insular species the ranges are 500 miles or less in extent; half of them have ranges which cover less than 2000 square miles. Half of the continental forms have ranges of more than 200,000 square miles. Since the size of a range has some relation to, even if it is not an exact parallel of, the number of individuals involved it may be said that continental species usually represent a hundred times as many individuals as insular species. The largest continental species may involve 15,000 times as many individuals as the smallest insular species. These great differences in the sizes of specific populations are the primary bases of the differences in their evolutionary histories.

The individual variation found in these insects has been recorded in other publications.[6-9] If, in summary, we put the species in five groups according to the extent of variation within each, we have the following data:

	SPECIES STUDIED	VERY CONSTANT	FAIRLY CONSTANT	VARIABLE	HIGHLY VARIABLE	MOST EXTREME
Insular Species	158	82%	12%	4%	. .	2%
Continental Species	39	. .	13%	74%	13%	. . .

Four-fifths of the insular species are more constant than any of the continental species; four-fifths of the continental species are distinctly variable; and yet the three most extreme instances of intra-specific variation occur among what are distinctly insular species from the mountains of Colorado and Utah. The uniformity usually found among the insular forms appears to depend upon the smaller sizes of the populations involved. Other factors being uniform, there is less chance that major mutations will appear in small populations. Again, as Wright has emphasized (1931),

near homogeneity should be reached more quickly in a small, freely inter-breeding population than in a large, partially subdivided group. To a large extent the hypothesis is verified by the facts; but as with all con-siderations of chance, the analyses of specific cases show that the un-expected may sometimes happen, resulting in this case in intra-specific variation among a few of these island forms which equals or surpasses that found in continental Cynipidae.

In 94% of the continental cases, intergrading populations were found to occur between related species. Intergrades were found in only 12% of the insular species. It is to be recalled that Darwin and his contemporaries were peculiarly ignorant of the existence of inter-specific intergrades. Re-cently, however, the more thorough taxonomic studies are so often in accord in finding intergrades that the opinion is now current that this is characteristic of all species. The studies on which this opinion is based are, however, largely concerned with continental forms, and the cynipid data show how much continental and insular species may differ in this regard.

The interpretation of these intergrading series between species is crucial for the understanding of evolutionary processes. In the Darwinian theory, and to most taxonomists today, they represent the transitional stages in an accumulative variation by means of which the one species has evolved from the other in the series. But the absence of intergrades between insular forms indicates the need for some better explanation of their occurrence in continental areas. As I have elsewhere shown,[8,9] the differ-entiation of these insular species of gall wasps often involves such startling changes as the nearly complete loss of wings, the doubling or tripling in length of abdominal spines, the reduction of the whole thorax even to a half of its former size, the change from leaf to stem oviposition, striking changes in gall characters and changes in the choice of host. The differ-ences between the most closely related Cynipidae are sometimes of such magnitude that they would rate as generic in most taxonomic practice. With such distinct characters and so many species involved, it seems improbable that intergradent types could ever have existed without leaving more evidence than we find among the insular forms today. Muta-tion and not accumulative variation seems to have been responsible for most of the evolution among insular groups.

Similarly it may be believed that the continental species of these same phylogenetic lines, differentiated as they are on essentially the same bases as their insular relatives, evolved in the first place as the result of mutation. But in these continental areas the opportunity for inter-specific hybridiza-tion has led to the development of large hybrid populations which lie between the original species. As I have shown in the two publications on Cynips,[8,9] the characters of these intergrading populations are precisely

what would be expected from crosses of the parental types when multiple factors are involved. Other workers find hybrid populations among other plants and animals which are located in the same portion of the United States from which we have these hybrid Cynipidae. And the final confirmation of this analysis comes from the experimental extraction of the parental stocks or synthetic production of the wild type hybrids by Anderson for species of iris,[11,12] Anderson and Woodson for several species of Tradescantia,[5] Mrs. Erlanson for roses,[13] Sumner for mice.[14,15]

In only 9 cases do the gall wasp hybrids constitute such large populations, with such uniform ranges and means of variation that they fit our definition of species as *populations having access to common stocks of genes.* The experimentalists are, however, inclined to believe that hybridization is a prime source of new types in evolution. It is again to be noted that this conclusion has been drawn from studies made in the eastern half of the continent, or from free-moving forms which are continental in nature even in the desert and mountain areas of the western portion of North America. The data do not justify the conclusion that hybridization is of great importance among insular species.

Local differences in remote portions of specific populations are characteristic of continental but rarely found in insular species.

	SPECIES STUDIED	LOCAL RACES
Insular	158	5 = 3.2%
Continental	48	17 = 35.4%

It may be expected that more adequate material will show local races occurring in many more Cynipidae than the 22 recorded above; but the distribution of the cases which we do have seems significant. There is some current opinion that local races are to be found in nearly all species. The taxonomic and genetic studies (Anderson and Woodson 1935, Dobzhansky 1933, Sumner 1934, Wright 1932) are, however, based on forms that are largely continental and not representative of that large portion of the fauna and flora which is insular in nature. The rarity of local races among insular species is clearly another consequence of the small numbers of individuals involved. In small ranges there are few physical barriers to the free and rapid interchange of genes. In the wider-spreading continental species ecologic diversities, numerous physical barriers and (probably most important of all) distance may serve as partial barriers to the ready spread of the new characters which develop in locally segregated portions of the range.

The partial isolation of portions of continental populations leads to the current conclusion that the multiplication of species is most often achieved through a subdivision of the parental range. I have tried to analyze the gall wasp material on this point; but from the field data it is

not always easy to recognize whether it is subdivision of the old range or migration of the new type to a previously unoccupied area that has accomplished the speciation. The clearest case would be one in which the derived species was more or less surrounded by the older species. Among all the Cynipidae studied, there is not a single case of this sort. Another source of evidence, however, would lie in those species which split the range of the most closely related species. The species with the discontinuous ranges may be interpreted as parental species. There are only 3 such instances among the studied Cynipidae. They all occur in continental areas, in the eastern half of the United States. Beyond these cases, it is quite possible that some of the isolated species in the insular areas represent diverse developments in what was originally a single population ranging over the several islands now occupied by the set of species. I have not discovered a good method for recognizing such a history on the basis of the field data.

On the other hand, there is some reason for believing that most of these insular species have originated on the periphery instead of in the heart of the parental range, or, more often, have moved out of the parental range into territory previously uninhabited by that specific stock. In making the phylogenetic maps for the genus *Cynips*, it has often been possible to recognize which are the older and which the derived species. In almost every instance in insular areas the younger species occupies territory (either geographic or host) removed and even remote from the areas previously occupied by the older stocks. It is notable that in his thorough analysis of the cave cricket genus *Ceuthophilus*, Hubbell (1936) reaches the same conclusion as to the development of new species on the periphery of the older ranges. On the other hand, in continental areas the phylogenetic chains in *Cynips* turn in every direction, with little geographic trend, and it is possible that in such areas subdivision of the parental ranges is a more common source of the multiplication of species.

In summary, it may be remarked that it is unfortunate that continental species have been the best known among both European and American biologists. The conditions which have made it possible for certain forms to become continental have made it inevitable that students should first of all have explored Central Europe and the eastern third of the North American continent; the very factors which have isolated insular species have removed them from the attention of the laboratory investigator. Current concepts of species as highly variable, locally sub-divided, widely intergrading populations are based upon and quite justified by the data on continental species. But among these the significance of mutation is largely concealed, and the significance of hybridization as a factor in evolution is greatly over-emphasized. Insular species, which are in actuality very common among many groups of plants and animals, are

usually quite homogeneous in constitution, show little tendency for sub-division into local populations and give rise to few inter-specific hybrids. They indicate that mutation and the early isolation of the new types are important means of increase in the number of species. In any event, insular species are simpler to interpret, and an understanding of such forms may be basic to an understanding of continental species.

[1] Contribution from the Zoölogical Laboratories of Indiana University No. 263 (Entomological No. 17).

[2] Dunn, *The Salamanders of the Family Plethodontidae*, Smith College (1926).

[3] Hubbell, *Univ. Fla. Biol. Ser.* 2 (1936).

[4] Fernald, *Mem. Amer. Acad. Arts Sci.*, **17**, 1–183 (1932).

[5] Anderson and Woodson, *Contrib. Arnold Arboretum*, **9**, 1–132 (1935).

[6] Kinsey, *Ind. Univ. Studies*, 53 (1922).

[7] Kinsey, *Ind. Univ. Studies*, 58 (1923).

[8] Kinsey, *Ind. Univ. Studies*, 84–86 (1930).

[9] Kinsey, *Ind. Univ. Sci. Ser.*, 4 (1936).

[10] Wright, *Genetics*, **16**, 97–159 (1931).

[11] Anderson, *Ann. Mo. Bot. Gard.*, **15**, 241–332 (1928).

[12] Anderson, *Ann. Mo. Bot. Gard.*, **23**, 457–509 (1923).

[13] Erlanson, *Mich. Acad. Sci., Arts, Letters*, **5**, 77–94 (1925); *Rhodora*, **30**, 109–121 (1928).

[14] Sumner, *Proc. Nat. Acad. Sci.*, **15**, 481–493 (1929).

[15] Sumner, *Amer. Nat.*, **68**, 137–149 (1934).

[16] Dobzhansky, *Amer. Nat.*, **67**, 97–126 (1933).

[17] Wright, *Proc. 6th Intern. Congr. Genetics*, **1**, 356–366 (1932).

ON THE INTEGRATION OF OPERATORS

By GARRETT BIRKHOFF

HARVARD UNIVERSITY

Communicated December 5, 1936

Suppose one is given a system of ordinary differential equations having the special form

$$dx_i/dt = \sum_{h=1}^{r} \rho_h(t) \cdot X_i^h(x_1, \cdots, x_n) \quad [i = 1, \cdots, n]. \tag{1}$$

We propose the question: how can one find a vector-field Z such that if $x(t)$ is any solution of (1), if $y(t)$ is any solution of

$$dy_i/dt = Z_i(y_1, \cdots, y_n) \tag{2}$$

and if $x_i(0) = y_i(0)$ for $i = 1, \ldots, n$, then $x_i(1) = y_i(1)$ for $i = 1, \ldots, n$?

If one regards the vector-fields $X^1, \ldots, X^r$ as infinitesimal transformations in the sense of Lie, one sees that this question is a special instance of the following more general problem.