

DETERMINATE EVOLUTION IN THE COLOR-
PATTERN OF THE LADY-BEETLES

BY

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PART I.

INTRODUCTORY CONSIDERATIONS.

The lady-beetles were considered desirable for this study because their variability, distribution, and taxonomy indicated that they had been recently and are probably now in an active state of evolution. The practical advantage that they could be obtained in considerable numbers from many localities and could be experimentally bred was, then, decisive in their favor.

All of the American coccinellids which could be obtained in numbers and which showed a variable color-pattern were studied, viz, Hippodamini, Coccinellæ, and Epilachnini, divisions employed by Casey (1899).

The Epilachnini differ from the rest of the family in being leaf-eating, in having longer generations, and in hibernating necessarily in the winter; whereas the other coccinellids which eat aphids, fungus spores, and pollen will remain active during the winter in a vivarium and give many more generations. The difficulties of keeping a large and constant stock of aphids on hand and keeping the beetles free from diseases, especially such as result from dampness in the late summer and irregular temperatures in the winter, proved to be very serious and prematurely shortened many pedigrees. These difficulties also decreased the numbers which could be successfully managed. Nearly all the pedigrees, however, are given, for when too fragmentary to have much value in the study of dominance and segregation, they are, nevertheless, of value in showing the transmissibility of some characters and variation from the parent.

The dorsal color-pattern in all the American species within these groups is given for the sake of completeness, although for some species but little variation data was obtainable. This fact, together with the necessity of carrying in mind the data of variation and distribution in discussing experiments upon any given species, has led me to arrange the presentation according to species, after this introductory section. Furthermore, this arrangement will be more advantageous for those whose interest in this contribution is primarily taxonomic.

Every considerable new accession of data involves another revision of these tribes, since there has been so much disagreement among the authors and since the lines between varieties and species in these remarkable genera are so doubtful. I am obliged, therefore, to present a revision of my own in order to have a suitable nomenclature. Since the revision is not an end in itself, I have not given full descriptions, but only discussed and illustrated the color-pattern of the parts studied, although of course the revision is based upon many characteristics.

Not having studied the structural features of the foreign species, I have not ventured to revise the genera and have simply adopted the genera as used by Casey.

The differences in sculpture of the elytra have not been found to have the constancy and systematic value which some of the earlier writers have placed upon them. The variation is, moreover, largely ontogenetic, as I have observed in the pedigreed material. The shape of the elytra must also be used with considerable caution, because of its variability, as shown in table 2, and the optical illusions from the angle at which they harden and from the longitudinality or the reverse of the pattern.

The sex of the individuals has in most cases been observed; always in the experiments. The same sex is not the more heavily pigmented in every species. The sexes are not given separately except where the difference was obviously significant. The color-patterns of the larvæ have been used in evaluating relationships in some cases, but their description is outside the field of this paper.

The numbering of the elytral spots employed in *Hippodamia convergens* follows Weise, not Kellogg and Bell (see figs. 3, *b*, and 17). In other genera a corresponding system is employed: + is used to indicate confluence, *ap* to indicate a close approach to confluence, *sl+* for a very slight confluence, and *tr* for transition between separateness and confluence.

Formulæ are used where possible to designate unnamed varieties; in other cases it has been necessary to use letters. New names have been given to varieties only when they are common, distinct, and frequently collected, so that a name is needed.

PRINCIPLES OF CLASSIFICATION.

There is an improper demand for finality of treatment on the part of many systematists. These workers wish to use a treatise almost solely for the purpose of definitely dividing their collected specimens into categories. Such a demand leads many systematic writers to a false positiveness in regard to distinctions and evaluations. Many revisions are thus led to present a precision and show of finality which is not justified. New names involving new distinctions are valuable, but the reviser who fails to bring to light the points of doubt and uncertainty as well is negligent. A revision should give questions as well as answers; it should not only shed light, but indicate where more light is needed. To assume surety on an inadequate basis is inimical to the advance of science. On the other hand, there are some who go to the other extreme and hesitate about calling attention to an apparently new species, or some other difference, until they feel wholly assured. This policy retards progress and may result in the information never being made public because of the intervening death, incapacity, or disinclination of the investigator. An impression based upon extensive special knowledge has scientific value, provided it is avowedly only an impression. I have not sought, therefore, in this revision any degree of finality, but have tried to adopt a nomenclature which, from

present data, seems the nearest approximation I can make to the true condition, for I well know that its usefulness will soon be past.

I believe that it is very important that the International Congress of Zoologists should adopt a set of definitions of species and the less inclusive taxonomic grades in order that some uniformity can be attained in the use of such words as varieties, subspecies, forms, aberrations, mutations, etc. Until that time each writer must define his use of such terms whenever called upon to use them extensively. Failure to do this is causing a constantly growing confusion.

The following definitions will show the meaning of the terms as here employed. I am well aware that many of these terms are used differently by some writers, but at present each worker can merely choose the use that seems most satisfactory to him.

A species consists of individuals which, aside from sex, age, and periodic differences, have a fundamental similarity and which are habitually and successfully interbreeding. They comprise an intergenerating unit.

A section is a part of a species which is cut off by some barrier from intergeneration. Where the individuals of the section have no apparent difference from the mass of the species the section is ignored. Where the difference is so great that individuals of the two sections are always readily distinguished, a distinctive name becomes desirable and the form is considered another species rather than a section, although experimentally the two will interbreed freely. The difference between section and species is one only of degree of difference in the characteristics. The section may be found to be ontogenetic or phylogenetic in its nature.

A subspecies is a part of a species which inhabits only a portion of the range of the species and which, while differing in some appreciable respect, intergrades with it in the intermediate region. At any one point throughout the range of the species the quantitative expression of the chief differential of a number of individuals similar in age, sex, and season should give a unimodal polygon of frequency. The term "subspecies" may be used without reference to the inheritability of the differences. But where these differences are found primarily because they are the result of environment in each generation, the subspecies is called an ontogenetic subspecies. Where it is present primarily because inherited it is called a phylogenetic subspecies.

If the conditions of a subspecies are fulfilled, except that the individuals in question are scattered geographically and are confined to a particular kind of habitat throughout its range, then we have a habitat-form, which may be ontogenetic or phylogenetic. The usual assumption that all habitat-forms are ontogenetic is, I think, questionable, although they are probably generally so. The distinction between a subspecies and a habitat-form is not a sharp one, for a subspecies is a habitat-form where the habitat involves a very large, continuous area. The habitat-form falls

short of a subspecies when the habitat is made up of many discontinuous areas surrounded by a population of the contrasted forms.

A variety is a part of the species which differs from the typical members of the species by some hiatus which can be detected by the decreased number or absence of intergrades. When some considerable imperfection of the interfertility of the apparent variety and the typical species is found or some other cause makes their interbreeding uncommon, the variety becomes a species. Only an arbitrary line can be drawn, and to make an arbitrarily definite one would be infeasible at the present stage of our science. The variety may be equally common throughout the range of the species; it may be much more common in one part; it may be limited to one part of the range; or it may wholly replace the species in one part of the range. If its frequency only gradually changes in one direction, a subspecies is there constituted. If the variety is confined to a particular habitat, we have a habitat-variety.

An aberration is an individual which is wholly unique, generally pathological in origin, and often unsymmetrical. Where the character is symmetrical and there are no pathological appearances or the variation is of a sort found normally in other species, the specimen is probably one of a rare variety rather than an aberration.

A mutation is a specimen of a variety which is known to be capable of hereditary transmission, but the ancestors of which are typical individuals of the species. Where this information is lacking the apparent mutation can only be considered to be a rare variety, the origin of which is probably traceable to a progenitor more or less remote.

An extreme fluctuant is an individual which appears sufficiently different to be noticeable, but is, nevertheless, only an extreme case of the ordinary fluctuation, as is shown by the greater frequency of the intermediate conditions.

Form is a term of convenience only, applied to differences the real nature of which is in question. Many forms will later be found to be extreme fluctuants, others may represent points in a fluctuating series easily recognized or described, while still others are doubtless real positions of organic stability, which further study will show to be varieties or intermediate conditions between varieties and continuous variations.

STRUCTURE OF PIGMENTED AREAS.

I have limited the work, with a few exceptions, to the color-pattern, because with the other characters we have for the most part stable conditions with only a little fluctuating variation. For the further advantages of specialization I have concentrated my attention upon the pronotum and elytron. I believe, however, that similar results would have resulted were the study extended to include the coloration of the larva and the remaining parts of the imago. The coloration of the pupa, however, is much more subject to modification.

That the attachments of the muscles have an influence on the color-pattern of the head and pronotum is probable. I have not felt it necessary to go into the matter of structure of these parts in detail, however, because the great range of variation in the color-pattern within a genus, or even within a species, where the structure could not differ in any but a slight degree, is such that the influence of structure can be only along narrow lines.

In the elytra the influence of structure is more evident, but less than might be expected. The sutural margin is thickened and paralleled by a slight groove. As will be seen later, this margin is especially subject to pigmentation, and this in fact distinguishes several species and varieties. Spots are confluent with it in a few species and may become so by modification by cold in *Hippodamia convergens*. Yet, in general, when spots near the suture enlarge, their margins, which if they remained circular would become tangent to the suture, flatten and become parallel to the suture without touching it.

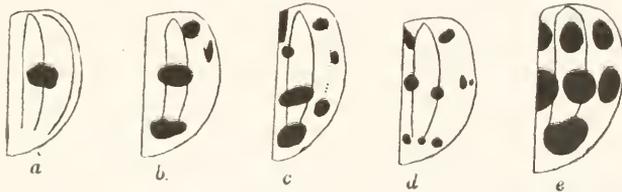


FIG. 1.—Position of linea interna, linea media, and linea externa, of: a, *Adalia*; b, *Coccinella*; c, *Hippodamia*; d, *Analis*; e, *Epitachna*.

The lateral and basal margin is much modified structurally in variations of germinal origin. It is one of the parts least subject to pigmentation. In modification by cold, however, pigment readily extends along it from neighboring spots.

In *Adalia* three veins are visible, named by Schroeder (1901) linea interna, linea media, and linea externa (fig. 1). The linea externa is quite close to the reflexed margin. It departs farthest at the humeral angle, where it can be most clearly seen. Any other veins that exist must be in the modified and thickened sutural or marginal parts of the elytra. The influence of these lines on the color-pattern of *Adalia* is considerable, as shown by Schroeder (1901).

But in *Coccinella* the linea externa can not be seen in the hardened elytron; yet its path can be traced in the basal half of the elytra by the extension of pigment along its course in *C. novemnotata* from the spots 1 and 2 along the linea externa. This is farther from the margin than in *Adalia*. It is probable that there is a vein in the soft elytron, visible evidence of which (to the hand-lens) does not persist in the mature wing.

In *Hippodamia* also the linea externa is not visible. Its course is outlined by pigment in cases of modification by cold and in the two wild

specimens shown in figs. 25, 16, *aa*, and 16, *bb*. In *Epilachna* and *Anatis* it is not visible and no cases were seen of pigment disturbance.

Pigment follows along the veins readily, especially along the *linea externa*, in cases of increase of pigment by modification; but in varieties of spotted species of germinal constitution the influence of veins is not great. The *vittæ* when present are frequently at an angle to the course of the veins or broader upon one side of it than the other. Transverse confluence, which is not influenced by any elytral structures, is more common than *vittæ*.

There is pressure upon the elytron from below at the humeral spot by the basal attachment of the wing below, at the site of spot *e* by a projection of the thoracic plates, at and near the site of spots 4 and 5 by the folding of the wings beneath, and at spot 6 by the tip of the abdomen when bent back, as it frequently is. Nevertheless these spots are not infrequently absent and there is no especial pressure where other spots are present. From these considerations and the well-known theoretical objections to kinetogenetic origins of germinal characteristics, I am not disposed to see any causal relation between pressure from below and the position of the spots, although the coincidence is striking in the second case.

DEVELOPMENT OF PIGMENTED AREAS.

The color-pattern of the head and thorax are fully formed at time of emergence. The black pattern of the elytra is formed subsequently. The soft, freshly expanded elytra are free from all black pigment. This is true in all the species which I saw emerge, including *Epilachna borealis*, of which the contrary has been stated.

No sequence in the appearance of spots could be positively determined, so nearly simultaneous is their development and so gradual is their appearance. Where the pattern is composed of strongly confluent spots, the pattern appeared at once, though not at first of full intensity, without passing through a separate spot stage. The pigment area, however, increased slightly during the few successive days after emergence before the elytra were fully hardened. This extension was so slight that it would not have been detected but that the pattern of a few freshly-emerged beetles, the pigment of which had become fully black, were described as having spots 1 and 3 very close together, but separate. Several days later they were found to be slightly confluent. Confluence of this kind, however, is only seen where the contiguous spots are unduly large and is the result of a mere enlargement of spots. Their inheritance is like that of an extreme fluctuant, as shown in pedigree table 15. Confluence, therefore, is of two kinds. In confluence of the hereditary type, the spots may be quite small and distant, as in *Epilachna corrupta*.

THE UTILITY OF THE COLOR-PATTERN.

The utility of the color-pattern is obviously not that of protective resemblance, for it is decidedly conspicuous in the green surroundings which the beetles frequent. This conspicuousness is generally thought to be explicable as a result of the habit these beetles have when disturbed of expelling a disagreeable fluid from the ends of the femora. The possession of a striking and peculiar appearance, by which the bird or other predaceous animal might associate this painful experience, would obviously be advantageous. In Poulton's terminology the color is aposematic. The only other explanation that seems at all plausible is that of sexual attractiveness, *i. e.*, the color is epigamic. The apparent indifference with which *Hippodamia convergens*, spotted or unspotted, breed together at Berkeley, California, although both forms are common there, makes this unlikely. I collected a number of mating pairs and could see no evidence for either assortative or preferential mating, in this confirming Kellogg, who also collected a number of mating pairs and reached the same conclusion.

The explanation of the ground-color of these beetles as warning or aposematic may be accepted upon the following evidence from Judd (1899), based upon extensive examinations of the stomachs of birds:

In the Coccinellidæ we have showy insects, ill-scented or flavored, that are eaten by but very few birds—the flycatchers and swallows; and hence here is a whole family which conforms well with the theory of warning coloration. * * * The showy, ill-flavored Coccinellidæ [are] * * * almost as * * * highly protected from birds as the hairy caterpillars and the elm leaf-beetle.

To this may be added my attempt to feed *Coccinella novemnotata* to a catbird reared in captivity. The bird took the beetle up to its perch, but then dropped it. The beetle walked away without further molestation.

Since Judd finds that the barred and spotless species as well as the spotted species are protected, the particular patterns can be of little importance, although they are so diverse. In flight, where the beetles are most attacked, the pattern is inconspicuous, while the ground-color is evident. But what is quite conclusive is the origin and persistence of varieties having fundamental differences from the pattern of the spots of the parent species. The fundamental usefulness of an aposematic pattern would depend, above all, upon its constancy. If the spotted pattern, which is so widespread in the family and is the primitive pattern for many genera or subgenera, has a strong association value with distastefulness, all departures from it would be suicidal; yet we find they are not. It is certain, then, that there is no high selective value in the spotted pattern, but it is possible that there is a feeble one. The loss of the spots or their change into other patterns must, then, be the result of some stronger evolutionary force, which I believe to be determinate evolution, overcoming the slight advantage placed on spottedness by natural selection.

This cause will be discussed after the presentation of the data. It is referred to here that the reader may bear in mind the question of utility *versus* determinate evolution as the species and varieties are described.

LIFE AND HABITS.

It is not necessary to give any detailed account of the habits of these insects for the purpose of this article. Only those features will be selected that are significant for this discussion of the color-evolution. Lady-beetles are probably well protected from predaceous animals by their distastefulness, as shown by the experiment with the catbird. In the localities where they are abundant I have never seen them attacked. Frequent causes of death are parasitism by internal insect larvæ, an unknown disease, and difficulty in casting the larval skins on emergence from the pupa; but the two great causes of death are hibernation and the maldistribution of eggs. Any considerable advantage in either of these respects would be strongly favored by natural selection.

Epilachna is uncommon in the spring at Cold Spring Harbor until the new brood comes forth, when it is quite abundant. Efforts to hibernate it under as favorable conditions as I could arrange succeeded in not more than 50 per cent of the individuals. Attempted hibernation with other species was unsuccessful, although some, when provided with food, overlived the winter in the vivarium. The critical conditions seem to be extremes of dryness and moisture. *Megilla maculata* hibernates, at least frequently, in masses, one of which was found and kindly sent me by Dr. Robert W. Hall, of Lehigh University. I am assured by Prof. N. F. Davis, of Bucknell College, that in the spring such a mass was seen to mount a fence-post preparatory to flight. In the Western States *Hippodamia convergens* and *spuria* resort to the same practice. Strangely enough, such masses were frequently found on mountain-tops throughout the Western States. This is probably not adaptive, but a by-product of some tropisms. These beetles are found in great numbers in the flotsam of the shore of large bodies of water when a certain sequence of winds occurs during the time when large numbers are in their long flight. The ability to collect large numbers on mountain-tops and shores has been a favoring circumstance to the collection of material for this paper. I would like here to solicit the opportunity of examining any such masses, and I will gladly return them if desired.

While these beetles fly very little in cloudy weather, on warm sunny days they frequently take long flights. This is important as breaking down the probability of isolation, widening the range of varieties, and making their passage into species more difficult. Dispersal is probably even more effective than in birds, which have such powerful homing instincts, although of course the occasional storm-driven bird frequently gets much farther astray.

The food of these beetles is well known to consist principally of aphids. Certain coccids are eaten by some of the species, but this is the exception. A coccid of the chestnut constitutes one of the principal foods of *Cycloneda munda* at Cold Spring Harbor. This coccid is not eaten by any of the other species. *Megilla fuscilabris* is also peculiar in its food habits, for it eats a much larger proportion of pollen and fungus spores than are eaten by the other species. In general, coccinellids eat a wide range of species of aphids. Some species of aphids are found to be especially attacked by some species of lady-beetles; thus, that of *Rhamnus cathartica* apparently is attacked only by *Adalia bipunctata* at Cold Spring Harbor. This may be partly attributable to its early and short season. Upon the willow, *Adalia bipunctata*, with only rarely a specimen of *Harmonia picta*, is found on Long Island. The preference of *Coccinella monticola* for the larch has been observed by Dr. G. W. Dimmock. At Cheney, Washington, the aphid of the box-elder is especially attacked by *Adalia*. Other preferences of coccinellids outside of the groups here treated, such as those of *Chilocorus similis*, *Pentilia*, and *Vedalia*, are well known in the literature of economic entomology. The species of *Hippodamia* and *Coccinella*, however, show fewer preferences and are therefore found in more general competition. I have elsewhere published further data in regard to the food of lady-beetles. (Johnson, 1906.)

Epilachna, as is well known, differs in being solely a leaf-eater. In this genus the species differ more in their food, for *E. borealis* eats the leaves of the cucurbits, while *E. corrupta* eats those of the bean.

Sexual attraction is especially powerful in the lady-beetles, since so large a proportion of them are seen in copulation. This is partly due to the prolonged time of copulation. But when the pairs are associated, the male nearly always attempts mating at once. Mismatings of species with species and even family with family have been recorded more often, I think, in the coccinellids than in any other family. This is significant in connection with sexual selection, for, where promiscuity prevails, as it does here, the chance of either preferential or assortative mating is decreased. A female may lay fertile eggs as long as 3 months after mating and possibly longer. The beetles are emerging at intervals throughout the summer, the broods overlapping. Promiscuity is, therefore, an advantage in this species, for if the male did not mate or attempt to mate frequently, many of the females would lay batches of sterile eggs before being fertilized, as this is their habit when reared and not provided with mates.

The eggs are laid in successive batches of 1 to 40, most frequently about 20, at intervals of a few days for an extended period. The competition between the larvæ of one batch is frequently very severe, because the existence of the colony of aphids which excited the female to lay her eggs is vicissitudinous. Aphids suffer from attacks of lace-wing flies, syrphids, and diseases. The latter two causes of death are especially serious and frequently destroy a whole colony of aphids upon which a fraternity of

lady-beetle larvæ are feeding. These larvæ then disperse in search of another colony of aphids. In this they are rarely successful, for colonies of that species of aphid in the immediate neighborhood are subject to similar attacks and with the larva's limited capacity for wandering the chance of finding another species of aphids is indeed slight. As a consequence, more larvæ would be successfully reared if the females laid their eggs singly in good aphid territory, for large batches of suitable aphids are frequently seen without lady-beetle eggs or larvæ. Any change in this direction is not possible, however, because there are no favorable variations by which the lady-beetles could locate a sufficient number of colonies to distribute their eggs properly.

The less of two evils, then, is to risk overcrowding and the consequent failure of some of the batches. We ordinarily think of overcrowding as having no other result than the desirable one of the survival of the fittest, but this other result of group-suicide may and frequently does follow. I have often seen a batch of eggs laid on a plant where I could see that the colony of aphids could not last through the larval life of the coccinellids because of syrphids or attacks on the aphids of disease. The larvæ would then disappear among surrounding plants destitute of aphids. In *Epilachna*, on the other hand, the laying of eggs in batches is advantageous, for shortage of food-supply is unlikely. In confinement the larvæ, except those of *Epilachna*, are cannibalistic when the aphids are exhausted. This is probably not an important feature in nature, however, because the larvæ are so rapidly dispersed when the food is exhausted.

Although assortative mating is apparently not operative in these beetles, there is a very remarkable assortative association. At Oakland, California, the typical *Hippodamia convergens* and its spotless variety are both common, yet a hibernating mass taken by Mr. Nunenmacher and kindly given to me consists almost wholly of the spotted variety, as shown in table 6. If other hibernating masses are found to be similarly segregated we have a noteworthy condition. It is doubtful if this produces much or any passive assortative mating, however, as dispersive flights for food doubtless precede mating in the spring.

VARIATION AND HEREDITY OF BODY-LENGTH.

The variation in size in some of the species is really extraordinary. It is relatively slight in *Epilachna*, *Adalia*, *Harmonia*, *Anatis*, *Cycloneda*, *Paranaemia*, *Megilla*, and *Anisosticta*. But in *Hippodamia* and *Coccinella* *H. convergens* and *C. novemnotata* stand out as greatly more variable than their co-species (fig. 2). It is easy to see why *Epilachna* should not be so highly variable, since the food-supply rarely becomes short for the individual larva. The aphid supply is, on the other hand, very uncertain, and it is a great advantage for a species to undergo metamorphosis when the food falls short, even though undersized. But why are not all the aphidivorous species highly variable, then? Again we may say that *Adalia* is more constant because of its short larval period, which makes it less likely to suffer from limitation of the food-supply; but why, then, is the large *Anatis*

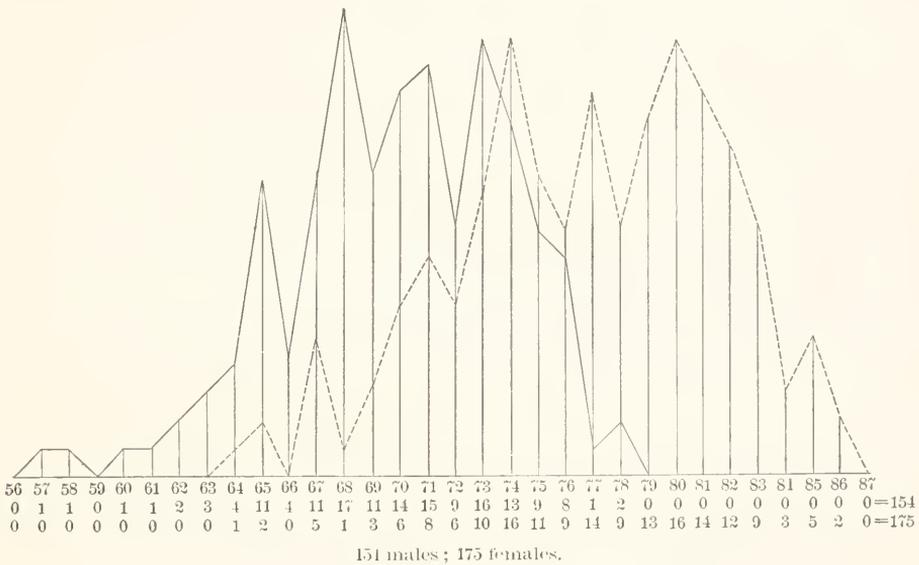


FIG. 2.—Variation of length of elytra of *Hippodamia convergens*, Fairfield, Washington, 1905.

relatively constant? To determine if shortage of food-supply really could reduce the size, I experimented upon *Epilachna*, which one would expect would be most resistant to such treatment. I was able to get healthy beetles of only 5.7 mm. in length of elytra, while 8.2 mm. is not rare in nature. I believe, then, that the greater part of the variation in size is modificational. In addition to the factors mentioned above, it seems possible that *H. convergens* and *C. novemnotata* resort to a greater variety of aphids, the season of some of which is of short duration.

ACKNOWLEDGMENTS.

Before proceeding with the detailed discussion of the species, I wish to express my gratitude to the owners or custodians of the following collections for the privilege of examining their beetles in these genera and in some cases for the loan of material: United States National Museum; Philadelphia Academy of Natural Sciences; American Museum of Natural History; Brooklyn Institute of Arts and Sciences; Museum of Comparative Zoology, Cambridge, Massachusetts; Boston Society of Natural History; Carnegie Museum of Pittsburg; University of Ohio; University of Missouri; University of Nevada (Prof. Peter Frandsen); F. Blanchard, Tyngsboro, Massachusetts; F. W. Bowditch, Brookline, Massachusetts; T. L. Casey, Washington, District of Columbia; W. T. Davis, New York; Charles Fuchs, Berkeley, California; L. H. Joutel, New York; C. W. Leng, New York; F. E. Lutz, Cold Spring Harbor, New York; W. S. Marshall, Madison, Wisconsin; F. W. Nunenmacher, Goldfield, Nevada; Carl Schaeffer, Brooklyn, New York; E. C. Van Dyke, San Francisco, California. I am further indebted to many friends who have sent me beetles from various localities. To the Director of the Station, Dr. Charles B. Davenport, my gratitude is due for my interest in evolutionary problems and for aid and encouragement in undertaking this one. I would also thank Dr. Schwarz, of the United States National Museum, for help with the German citations, and Prof. W. L. Tower for suggestions upon the structure of the elytra.

Except where otherwise stated, it is the intention of the author to deposit the types in the United States National Museum.

PART II.

THE DATA ARRANGED BY SPECIES.

TRIBE HIPPODAMINI.

Genus ANISOSTICTA Duponchel.

4033. *Anisosticta strigata* Thunberg.

Distribution: Northern States and Canada.

Var. *dohriana* Mulsant.

The subapical spot only free from the pattern of confluent spots. Typical specimens rare in North America, but have been taken on Vancouver Island.

Var. *btriangularis* Say.

Others than the apical spot free from the pattern of confluent spots. Most common in America.

Var. *A.*

Spots all separate. Manitoba; Sand Hills, Nebraska. These specimens probably represent a subspecies, for a specimen showing nearly as much separation came from Beaver Dam, Wisconsin. Specimens of the typical species of the variety *dohriana* are rare.

Var. *B.*

A specimen from Wyoming shows spots fused into two marks, except the juxtapatural spots, which are free.

Weise records 2 specimens of *A. novemdecimpunctata* var. *irregularis* with 1, 2, 3 + $\frac{1}{2}$, 4 + 5, 6 + the suture, 7 + 8, 9 (his numbering), from Oregon. This throws some doubt on the specific distinction between *A. novemdecimpunctata* and *strigata*. The difference in the elytral markings are certainly bridged over by our variations.

Genus NAEMIA Mulsant.

3034. *Nacmia seriata* Mulsant.

Distribution: Maritime regions of the eastern United States and southern California.

Form *a.* The spots separate, but the apical spot meets the suture.

Form *b.* Some of the spots separate, others united. Mulsant says the separation of the third spot from the ground is most frequent, followed by the separation of the third from the fourth.

Form *c.* Scutellar mark prolonged and extended to the second spot.

Subspecies of Florida:

Pigment reduced, so that the spots are not confluent. In this it is analogous to the subspecies *floridana* of *Megilla maculata*. Pronotal pattern resolved to 4 spots in some cases.

Subspecies litiginosa Mulsant.

Specimens from Southern California in the Leng collection have the spots less confluent longitudinally, but more so transversely. They also have the caudal white spot on pronotum larger.

Genus MACRONAEMIA Casey.

3035. *Macronaemia episcopalis* Kirby.

Distribution: Western States and Canada.

The pronotal pattern in a specimen from Assiniboin, Montana, and in another from Wyoming is reduced to 6 spots. Otherwise it is relatively constant.

Genus PARANAEMIA Casey.

3037. *Paranaemia vittigera* Mannerheim.

Distribution: Colorado, New Mexico, Arizona, California, and New Mexico.

Shows very little significant variation. Casey believes those of Colorado and Arizona to be more slender, but with similar coloration, and has called them *P. similis*.

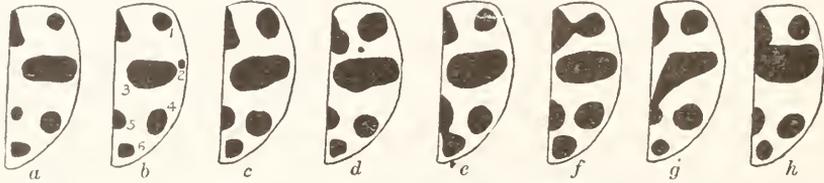


FIG. 3.—Variation of the elytral pattern of *Megilla maculata*. *c*=mode; *a* to *g* from Shawnee, Pennsylvania; *h* from Ohio and Texas.

Genus MEGILLA Mulsant.

3036. *Megilla maculata* DeGeer. (Figs. 3, 4.)

Distribution: United States and Canada, except Pacific coast.

This species is more constant than the other spotted Hippodamini (fig. 3), as indicated by the following count of 321 individuals from Shawnee, Pennsylvania.

Normal, 310.

Form *a*. The elytral spot at 3+4 on the suture resolved to a spot on each elytron free from the suture; 4 individuals.

Form *b*. 1 + scutellar mark; 2 individuals (fig. 3, *f*)

Form *c*. An extra spot between 1, 2, and the scutellar mark; 1 individual (fig. 3, *d*); 1 also seen at Cold Spring Harbor, New York.

Form *d*. 3 + 5; 1 individual (fig. 3, *g*); 1 also from Texas.

Form *e*. Spot 2 resolved into a larger internal and a smaller lateral spot (fig. 3, *b*).

There was a case of a slight deposition of pigment along the vein between 1 and 2 and in another between 4 and 6, in each case upon the right side only. Also one case of 2 + 3 on left side only.

Form *f*. Scutellar mark + 2. Not taken in the Shawnee lot, but 1 seen from Texas and 1 from Ohio (fig. 3, *h*).



FIG. 4.—Variation of the pronotal pattern of *Megilla maculata*. *b*=mode; *a* to *c*, from Shawnee, Pennsylvania.

The typical species is found only in Cuba. It has but one continuous area of black pigment upon the pronotum. The two subspecies following may be entitled to specific rank. The decision must wait for more extended collection in the Southeastern States.

Subspecies fuscilabris Casey.

The pronotum pattern has the two areas not confluent (fig. 4) and the spots not greatly reduced. This characterizes all of the North American range except the south-eastern States and Cuba. Casey believes that the specimens from South Texas are broader, with the color-pattern the same, and has named it *Megilla strenua*.

Subspecies floridana Leng.

Specimens from Beaufort, North Carolina, to Louisiana are smaller. The pigment much reduced, but the pronotum, although having the pigment reduced often to 4 spots may in other cases show a transverse confluence, in this respect approaching the typical species as found in Cuba.

Subjection to both 40° C. and 18° C. in the usual way failed to produce significant modification.

Genus CERATOMEGILLA Crotch.

3038. *Ceratomegilla ulkei* Crotch. (Fig. 5.)

Distribution: Hudson Bay.

A monotypic genus having unique antennæ and of obscure relationship. Apparently none have been taken since Ulke found the type at Hudson Bay. The drawing given (fig. 5) is pinned into the Leconte collection in the Museum of Comparative Zoology.

Genus ERIOPSIS Mulsant.

3040. *Eriopsis connexa* Germar.

Distribution: Texas, California, and Vancouver Island.

A South American species rarely found in the United States (fig. 6). It is possibly derived from a spotted *Hippodamia* by reversal of pattern. *E. eschscholzii* from Chili represents an intermediate condition comparable to *Hippodamia cockerelli*.

Genus HIPPODAMIA Mulsant.

The species of *Hippodamia* fall into several distinct phylogenetic sections, as shown in fig. 7 and table 1. The comparative size and form of some of the species of this genus are shown in table 2. While these differ, the ranges overlap to such an extent that size and shape are seldom serviceable in the identification of single specimens. The differences are large enough, however, so that the eye readily detects them in the comparison of series. The females are uniformly larger, but differ little in proportions from the males. Under *H. convergens* similar data will be given in regard to two of its varieties.

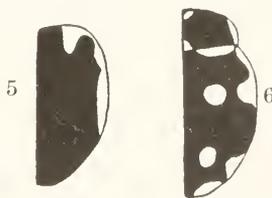


FIG. 5.—Flytral pattern in *Ceratomegilla ulkei*.

FIG. 6.—Flytral pattern in *Eriopsis connexa*, Texas.

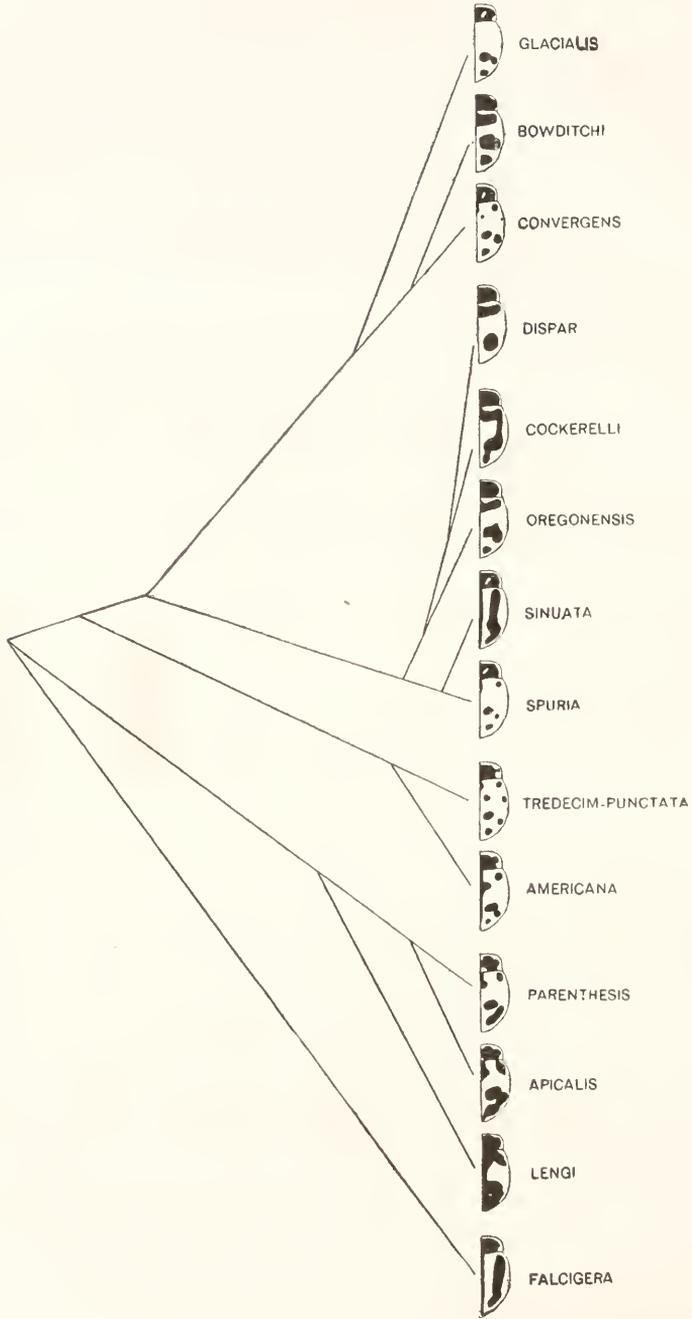


FIG. 7.—The species of *Hippodamia* in the United States.

TABLE 1.—*The species of Hippodamia.*

Group.	Species.	Locality.
Convergens.....	{ glacialis..... bowditchi..... convergens.....	Northeastern States and Canada. Northern Rocky Mountains. North America.
Spuria.....	{ cockerelli..... dispar..... oregonensis..... spuria..... sinuata.....	Rocky Mountains. Colorado. Cascade Mountains. Western States. China and Pacific States.
Septemmaculata variegata	{ variegata..... doubledayi..... bifurcata.....	
Tredecimpunctata.....	{ tredecimpunctata..... americana.....	Europe, Siberia, United States, Canada. Hudson Bay, Lake Superior.
Parenthesis.....	{ parenthesis..... apicalis..... lengi..... amoena..... arctaea.....	North America. Western States. Southern California. Eastern Siberia. Europe.
Incertæ sedis.....	{ fulcigera..... kreichbaumii..... racemosa.....	Hudson Bay, Great Stone Lake. Abyssinia.

TABLE 2.—*Comparison of mean and extreme dimensions of some species of Hippodamia.*

[Measurements, except those in percentage, expressed in units of 0.0625 mm.]

Species, sex, and locality.	No.	Length of right elytra.	Breadth of right elytra.	Breadth of right elytra in per cent of length of elytra.	Breadth of pronotum.	Breadth of pronotum in per cent of length of elytra.
H. convergens, Cold Spring Harbor:						
Male.....	37	66 76.9 83	25 30.6 36	31.5 40.1 47.5	36 41.1 44	48.5 57.4 59.5
Female.....	9	82 85.3 89	32 33.6 36	35.5 39.1 43.5	42 44.1 46	47.5 51.5 54.5
H. glacialis, Cold Spring Harbor:						
Male.....	26	78 86.3 94	28 35.4 41	34.5 41.2 46.5	41 46.6 51	50.5 54.2 59.5
Female.....	29	80 91.2 104	33 38.3 47	34.5 40.7 49.5	41 49.2 54	49.5 52.4 56
H. spuria, Kamiack Butte:						
Male.....	61	55 63.2 69	20 24.3 28	32.5 38.5 45.5	29 33.9 37	48.5 53.8 57.5
Female.....	75	54 68.2 73	21 26.4 31	32.5 38.7 44.5	29 35.5 39	47.5 52.1 56.5
H. parenthesis, Stony Lake:						
Male.....	53	56 59.9 61	19 24.2 29	32.5 40.5 46.5	30 33.7 37	51.5 56.3 60.5
Female.....	85	53 62.8 68	20 25.0 30	32.5 40.0 47.5	30 33.8 38	50.5 54.1 61.5

3044. *Hippodamia glacialis* Fabricius.*Distribution:* United States and Canada.

The color-pattern (fig. 8) of this species is approached and even realized in some cases by specimens of *H. convergens* in the Western States beyond the usually recognized range of *H. glacialis*. Yet complete intersterility was found to prevail in repeated tests between eastern specimens of the two species. Whether this intersterility is bridged over by these specimens in the Western States I was unable to test.

The resemblance of this species to *H. convergens*, and especially the similarity of their larvæ, is such that it has probably been derived from that older type at no very distant date. The pronotal pattern is like that of *H. convergens*, but shows relatively less variation (fig. 9).

Var. A. The humeral spot absent. In 9 out of 26, or 35 per cent of the males, and in 6 out of 29, or 21 per cent of the females at Cold Spring Harbor.

Var. B. Spots 4 + 5 + 6. Several taken from diverse localities. Nowhere established (fig. 8, *i*).

Var. C. Spots 6 + 4 + 5. As above (fig. 8, *h*).

Var. D. Spots 4, 5, and 6 merged in one rounded area (fig. 8, *j*). Only 1 specimen seen.

Var. E. With spot No. 2; 3 cases in 55, or 6 per cent, at Cold Spring Harbor (fig. 8, *a*).

Var. F. With the *extensa* mark. Only 1 specimen at Cold Spring Harbor (fig. 8, *g*).

Var. G. Spots 4, 5, 6 (fig. 8, *d*).

Var. H. Without discal spots on pronotum. Only 1 specimen from Cold Spring Harbor. Also seen in the *H. convergens* var. *pseudoglacialis* of the Western States.

Var. I. Median white spot upon head extending to eyes. Especially characteristic of western specimens (fig. 10).

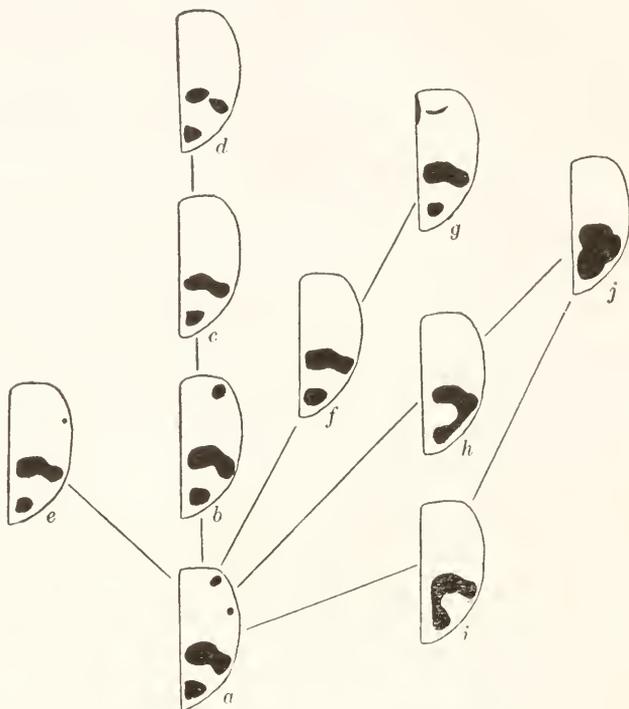


FIG. 8.—Variation of elytral pattern of *Hippodamia glacialis*.
b = mode.

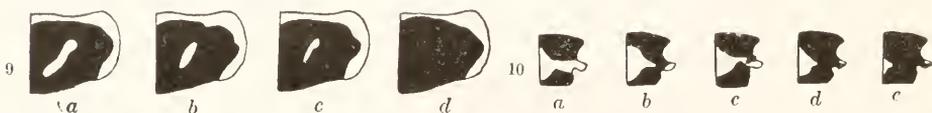


FIG. 9.—Variation of pronotal pattern of *Hippodamia glacialis*. b = mode.

FIG. 10.—Variation of color-pattern of head of *Hippodamia glacialis*. d = mode; a from Onaga, Kansas; c to e from Cold Spring Harbor, New York.

The appearance of spots 2 and 3 and of the scutellar mark, which is occasional, may be looked upon as reversionary. The *extensa* mark is also met with in *H. convergens* var. *extensa* and is a case of parallel variation.

HEREDITY.

The three females in table 3 with unknown mates show clearly enough that the presence or absence of spots 1 and 2 is inheritable. No. 453 had the transverse band broader than usual and its progeny show the inheritance of this condition, for in some of the offspring the mother was exceeded in this respect and none of them show the slightest tendency to the separation of the component parts. The heredity of spots 1 and 2 is segregative, with a few intergrades. The shortness of the pedigrees leaves the question of dominance unsettled.

TABLE 3.—*Heredity in Hippodamia glacialis.*

No.	Mother. Pattern.	No.	1			2		4 and 5	
			Present.	Very small.	Absent.	Present.	Absent.	Separate.	United.
248.	1 absent, 2 present, 4+5	8	3	0	5	7	1	3	5
434.	1 present, 2 absent, 4+5	31	25	3	3	0	31	0	31
453.	1 present, 2 absent, 1+5	11	13	0	1	0	14	0	14

3046. *Hippodamia convergens* Guerin.

Distribution: North America.

This is a wide-ranging species which is highly variable. For reasons given later I have thought it best to reduce to the status of varieties several of its derivatives which have received specific names. The variation (fig. 11) is strikingly parallel to that in *Hippodamia septempunctata* and to a less degree to that in *Adonia variegata*. The varieties of these two European species have been well studied and named. This is not the case with the American *H. convergens*. I have indicated the correspondence of these varieties by the sign of equivalence (\cong) used by mathematicians. The correlation of pronotal and elytral patterns is low enough to make it desirable to treat them separately.

Types of Patterns in Elytral Spots.

Spots $\frac{1}{2}$, 1, 2, 3, 4, 5, 6. Typical.

Spots $\frac{1}{2}$ + 3 + 1, 4 + 5, 6, var. *quinquesignata* Kirby.

Spots $\frac{1}{2}$ + 3 + 1, 4 + 5, 6, with pronotal discal spots, var. *puncticollis* Casey.

Spots $\frac{1}{2}$ + 3 + 1, 2, 4 + 5, 6, *H. septemmaculata* var. *continua*.

Spots $\frac{1}{2}$ + 3 + 1, 2, 4, 5, 6.

Spots $\frac{1}{2}$ + 3, 1, 2, 4 + 5, 6, var. *caseyi* (new variety) \cong *A. variegata* var. *ustulata* Weise.

\cong *H. tredecimpunctata* var. *contorta* Weise.

This common variety is generally called *lecontei* Mulsant, the description of which calls for a pattern quite different, which is given below. This variety is so well known that it seems best to rename it.

Var. *defecta* (new variety). Formula as in var. *caseyi*, but spot 1 small and 1 + 3 much less heavily pigmented.

Because of its interesting relation with var. *caseyi*, discussed later, this variety is given a name.

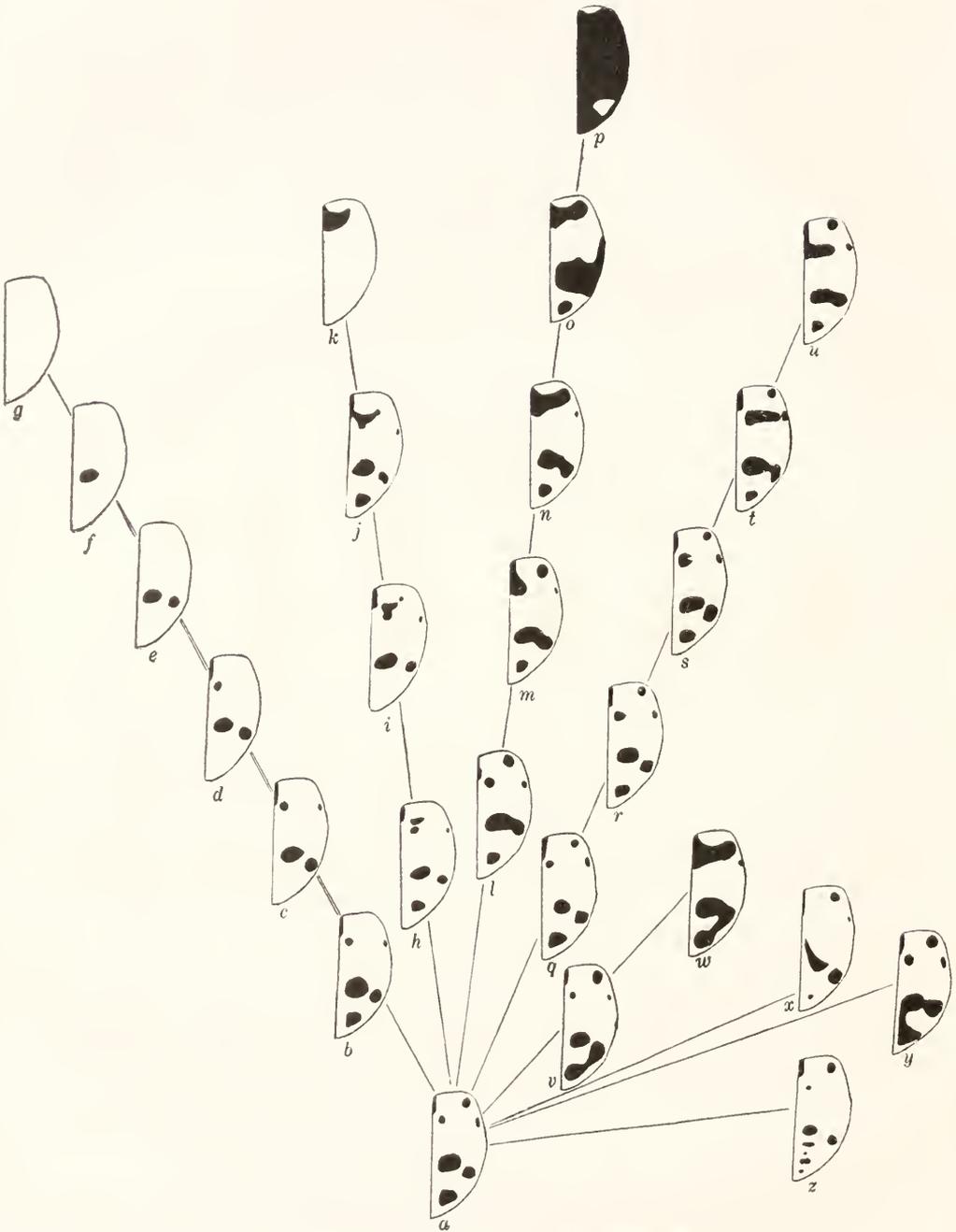


FIG. 11.—Variation of elytral pattern in *Hippodamia convergens*.

Spots $\frac{1}{2} + 3, 1, 4 + 5, 6$ = *H. septemmaculata* var. *viadri* Weise.

Spots $\frac{1}{2} + 3, 1, 2, 4, 5, 6$, = *H. septemmaculata* var. *paykulli* Weise = *H. tredecimpunctata* var. *triloba* Weise.

Spots $\frac{1}{2} + 3, 1, 4, 5, 6$, = *H. septemmaculata* var. *oblonga* Weise.

Spots $\frac{1}{2}, 1, 2, 3, 4, 5 + 6$, = *H. tredecimpunctata* var. *c. nigrum*; rare; California and Nevada.

Spots, $\frac{1}{2}, 1, 2, 3, 4, 5 + 6$, var. *juneta* Casey; taken in Sonoma County, California, and 1 specimen from Stony Lake, Michigan.

Spots $\frac{1}{2}, 1, 2, 3, 4 + 6, 5$, rare; Pacific States.

Spots $\frac{1}{2}, + 3 + 1, 2, 4 + 5 + 6$, rare; Rocky Mountains.

Spots $\frac{1}{2}, 1, 2, 3, 4 + 5, 6$ = *H. tredecimpunctata* var. *spissa* Weise = *H. septemmaculata* var. *aestiba*; common in Western States.

Spots $\frac{1}{2}, 1, 4 + 5, 6$, *pseudoglacialis* (new variety); New Mexico and northward.

Spots $\frac{1}{2} + 3 + e$, *extensa* Mulsant, Western States.

Spots $\frac{1}{2} + 3 + e$, 2, 4, 5, 6.

Spots $\frac{1}{2} + 3 + e$, 2, 4 + 5, 6.

Spots $\frac{1}{2} + 3, e, 2, 4, 5, 6$.

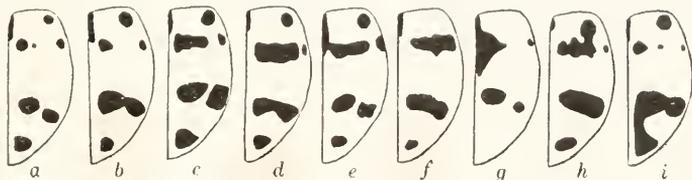


FIG. 12.—Variation of elytral pattern of the *quindecimmaculata* varieties. *c* = mode; *a*, from Lake Superior; *b*, California; *c*, St. Louis, Missouri; *d*, Iowa City, Iowa; *e*, Southern Illinois; *f*, Kamiack Butte, Washington; *h*, Keeler, California; *i*, St. Louis, Missouri.

Spots $\frac{1}{2} + 3, e, e', 2, 4, 5, 6$.

Spots $\frac{1}{2} + 3 + e + e', 4, 5, 6$, *lecontei* Mulsant.

Spots $\frac{1}{2}, 1, 2, 3 + q, 4, 5, 6$, *quindecimmaculata* Mulsant (fig. 12); Central States.

Spots $\frac{1}{2}, 1, 2, 3, q, 4, 5, 6$; very rare; Central States.

Spots $\frac{1}{2}, 1, 2, 3 + q + q', 4, 5, 6$, difficult to distinguish from $3 + q$, but known to exist from a few specimens with reduced pigment.

Spots $\frac{1}{2}, 1, 2, 3 + q, 4, 5, 6$, *quindecimmaculata A* Mulsant; very rare; Central States.

Spots $\frac{1}{2}, 1, 2, 3 + q, 4 + 5, 6$, *quindecimmaculata D* Mulsant; Missouri Valley; very rare.

Spots $\frac{1}{2}, 1, 2, \frac{1}{2} + 3 + q, 4, 5, 6$, *quindecimmaculata C* Mulsant; Missouri Valley; very rare.

Spots $\frac{1}{2} + 3 + q, 4, 5$; 1 specimen from Fairfield, Washington.

Spots $\frac{1}{2}, 1, 2 + q, 3, 4, 5, 6$; very rare; 1 specimen from Kamiack Butte, Washington, upon one side only.

Spots $\frac{1}{2}, 1, 2 + q + 3 + \frac{1}{2}, 4, 5, 6$; very rare; Missouri Valley.

Spots $\frac{1}{2}, 1 + q + 3, 2, 4 + 5, 6$; 2 specimens from Keeler, California, and St. Louis, Missouri, respectively.

With the comma-mark as in *Neoharmonia venusta* var. *A*.

Spots 1, 2, 3, 4, 5 = *septemmaculata* var. *vorax* Weise. Eastern as well as Western States.

Several spots lacking, *convergens C* Mulsant; Western States.

Mark $\frac{1}{2}$ only, *obsoleta* Leconte; Pacific States and Western Mexico. Most numerous in western Oregon outside the humid region. Extends in reduced numbers through Arizona to the Great Plains, giving way to var. *C* Mulsant gradually.

Spotless, with *obsoleta*; rare; = *H. tredecimpunctata* var. *signata* Fald. = *H. septemmaculata* var. *rubra* Weise.

Var. *moesta* Leconte:

The black area extended so as to leave only a small basal lunette and a small area between 4 and 6 of the reddish ground-color. Northern California to Vancouver Island and British Columbia between Hope and Okanogan. Limited to the humid Pacific Coast region. I have been unable to obtain living specimens. There is reasonable doubt as to whether this pattern may not constitute a distinct species, especially since at Dilley, Oregon, where the spotless variety prevails, one has been taken. It is clearly a melanic derivative from a spotted *Hippodamia*. Two specimens with pigment reduced enough to reveal the unobscured pattern are shown in fig. 13. While they do not agree in showing one direct line of development, it is probable that it is through var. *quinquesignata*. It is likely, moreover, that the beetles have some such pattern when newly emerged from the pupa, as Miss Isabel McCracken has shown for the melanic variety of *Melasoma scripta*, and that the variation in these when known will make the ancestry of var. *moesta* clear. The modification experiments upon *H. convergens* prove that a cold environment increases pigmentation. The degree of cold was such, however, that the beetles suffered more or less damage, and still they fell far short of the melanism of the variety *moesta*. Moisture alone produced no effect. For this reason and because Dilley, Oregon, has typical var. *moesta* rarely along with the spotless *H. convergens*, I believe that *H. moesta* is an inherited condition and not an "ontogenetic species." It remains to be seen whether it belongs to the intergenerating unit of *H. convergens* or not.

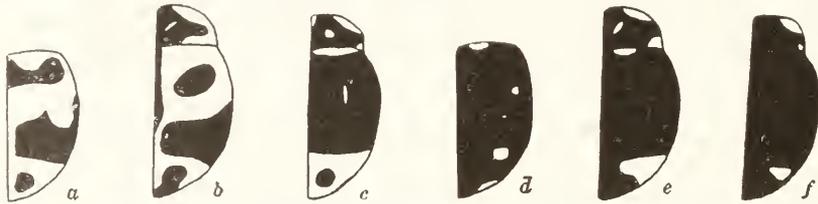


FIG. 13.—Variation of color-pattern of var. *moesta*, with two intergrades. *e* = mode; *b*, from Humboldt County, California.

Examination of these varieties shows that they are the several combinations of a number of characteristics, as follows:

- | | |
|--|--|
| 1 to 7. The mark $\frac{1}{2}$ and the spots 1, 2, | 11. The confluence of 1 and 3. |
| 3, 4, 5, 6, respectively. | 12. The confluence of 4 and 5. |
| 8. The new spot <i>e</i> . | 13. The confluence of 4 and 6. |
| 9. The new spot <i>q</i> . | 14. The confluence of 5 and 6. |
| 10. The confluence of $\frac{1}{2}$ and 3. | 15. The melanism of var. <i>moesta</i> . |

The combinations of these characteristics produce the different varieties given and the numerous ones not given, characterized by loss of certain spots. The distribution of some of the characteristics is given in tables 4 and 5.

The pronotum is subject to a similar remarkable variation (fig. 14), and this, strangely enough, is not highly correlated with the coloration of the elytra. Spotless elytra, as well as the typical spotted pattern, are associated with all or nearly all of the pronotal patterns. The typical pronotum is black, with 2 light convergent discal marks and a narrow light margin. The black area is slightly emarginate mesocephalad and the white margin is slightly narrower laterad and broader cephalolaterad and caudolaterad. The convergent marks may, on the one hand, disappear, or, on the other hand, break through to the margin, generally at a point in the continuation

of the direction of its greatest length. Occasionally it opens caudad of the lateral process and at other times at both places. Still more rarely it breaks through at a third point more directly cephalad. Table 5 shows the geographical distribution of these characteristics and its association with the elytral pattern.

As Kellogg and Bell (1904) have shown, the variation is continuous from large pronotal dashes through small ones to none at all. The presence or absence of pronotal dashes serves to distinguish specimens in collections from some localities, but not in the San Francisco Bay region.

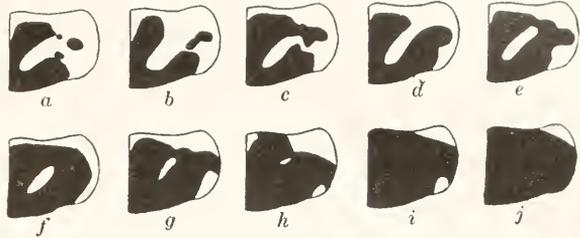


FIG. 14.—Variation of pronotal pattern. *a, b, d, e*, from Dilley, Oregon; *e*, Fairfield, Washington; *f* to *j*, Berkeley, California.

TABLE 4.—Elytral pattern in *Hippodamia convergens*.

Locality.	No.	Spotless.		Some spots absent.	12 spots present; no confluence.	4+5		1½+3		Var. extensa.		Var. quindecimmaculata.		Glacialis pattern.		
		P.ct.	P.ct.			P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	
Palo Alto, Cal. (K. and B.)	1,033	1—	6.09	93.6	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.	P.ct.
Kamnick Butte, Wash.	15,415	1—	15.3	84.6	6.3	36.2	3.7	8.0	1—	1—	0	0	0	0	0	0
Marsh Hill, Fairfield, Wash.	1,406	1—	33.7	66.3	37.9		2.4	9.8	0	0	0	0	0	0	0	0

TABLE 5.—Elytral pattern in *Hippodamia convergens*.

Locality.	No.	Per cent spotless.	Per cent some spots absent; no confluence.	Per cent typical spots present; no confluence.	Per cent some spots confluent.
Chewelah, Wash.	191	0	27.2	1—	72.2
Mount Carleton, Wash.	359	0	1—	0	99+
Spokane and Cheney, Wash.	107	0	58.8	5.6	35.5
Fairfield, Wash.	1,406	1—	33.7	8.6	50.2
Steptoe Butte, Wash.	573	0	81.3	0	18.6
Kamnick Butte, Wash.	15,415	1—	40.7	10.7	48.4
Goldendale, Wash.	159	0	11.9	84.9	3.1
Portland, Oreg.	10	0	10	90	0
Dilley, Oreg.	895	94.9	4.2	1—	0
Berkeley, Cal.	673	45.6	4.0	48.8	1—
Oakland, Cal., A.	632	9.2	1—	0	0
Oakland, Cal., B.	76	31.5	0	68.4	0
Watsonville, Cal.	68	51.4	6.3	48.5	0
Santa Clara Valley, Cal.	425	2.3	0	90.3	1—
Mendocino County, Cal.	84	0	3.5	96.4	0
Licking Fork, Cal.	17	5.8	70.5	23.5	0
Redlands, Cal.	71	12.6	1.4	85.9	0
San Diego, Cal.	4	75	0	25	0
Palo Alto, Cal.	1,033	1—	6.09	93.6	1.7
San José, Cal.	207	1.1	1.8	97.0	0
Coolidge, N. Mex.	75	0	14.6	32.0	53.3
Tepepam, Mexico.	201	5	17	78	1—
Bartlesville, Okla.	19	0	0	100	0
Stony Lake, Mich.	20	0	0	95	0
Cold Spring Harbor, N.Y.	203	0	1—	99+	1—

TABLE 6.—Variation of pronotum of *Hippodamia convergens*.

Locality.	Elytral spots.	No.	With dash.	With-out dash.	Marginal dash.			Margin.			
					Con-fluent cephalad.	Con-fluent laterad.	Con-fluent cephalad and laterad.	Com-plete and not con-fluent with dash.	Incom-plete cephalad.	Incom-plete laterad.	Incom-plete cephalad and laterad.
			<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>
Chewelah, Wash.....	Some a b-sent.	52	94	6	6			88	0	6	0
Do.....	Some con-fluent.	138	100	0	0	0	0	86	0	14	0
Mount Carlton, Wash.....	Do.....	139	99	1	1	0	0	41	0	58	0
Spokane and Cheney, Wash.....	Present.....	6	100	0	0	0	0	100	0	0	0
Do.....	Some a b-sent.	63	94	6	3	0	0	97	0	0	0
Do.....	Some con-fluent.	38	92	8	3	0	0	63	5	29	0
Fairfield, Wash., 1907.....	Present.....	14	100	0	0	0	0	100	0	0	0
Do.....	Some a b-sent.	94	97	3	1	0	0	98	1	0	0
Do.....	Some con-fluent.	143	100	0	1	0	0	11	0	88	0
Fairfield, Wash., 1907.....	Do.....	200	93	7	1	0	0	89	1	9	0
Steptoe Butte, Wash.....	Some a b-sent.	466	98	2	2	0	0	89	0	9	0
Do.....	Some con-fluent.	107	96	4	2	0	0	86	0	12	0
Kamlaek Butte, Wash.....	Present.....	118	97	3	1	0	0	88	0	11	0
Do.....	Some a b-sent.	2,372	96	4	4	1—	1—	96			
Do.....	Spots and 6 absent.	100	97	3	0	0	0	99	0	1	0
Do.....	Some con-fluent.	100	99	1	0	0	0	94	5	1	0
Goldendale, Wash.....	Present.....	154	100—	1—	0	0	0	100—	1—	0	0
Portland, Oreg.....	Absent.....	8	100	0	12	0	0	76	0	0	12
Dilley, Oreg.....	Some a b-sent.	38	100	0	5	0	2	74	0	10	0
Do.....	Absent.....	850	100—	1—	3	0	10	82	0	5	1—
Berkeley and Oakland, Cal.....	Present.....	383	100	1—	0	0	0	100	0	0	0
Do.....	Some a b-sent.	42	98	2	0	0	0	76	0	5	19
Do.....	Absent.....	756	42	58	1—	0	0	16	9	4	71
Watsonville, Cal.....	Present.....	33	100	0	0	0	0	94	0	0	6
Do.....	Absent.....	28	68	32	0	0	0	3	7	18	71
Santa Clara Valley, Cal.....	Present.....	643	100	0	0	0	0	700	0	0	0
Do.....	Some a b-sent.	32	97	3	0	0	0	97	0	0	3
Do.....	Absent.....	13	100	0	0	0	0	85	0	15	0
Mendocino County, Cal.....	Present.....	84	100	0	0	0	0	100	0	0	0
Licking Fork, Cal.....	Some a b-sent.	12	100	0	0	0	0	100	0	0	0
Do.....	Present.....	4	100	0	0	0	0	100	0	0	0
Redlands, Cal.....	Do.....	58	100	0	0	0	0	100	0	0	0
Do.....	Absent.....	4	50	50	0	0	0	0	0	0	100
Coolidge, N. Mex.....	Present.....	24	100	0	0	0	0	100	0	0	0
Do.....	Some a b-sent.	11	73	27	0	0	0	73	18	0	9
Do.....	Some con-fluent.	40	0	100	0	0	0	100	0	0	0
Durango, Colo.....	Do.....	19	37	63	0	0	0	21	21	11	47
Mitford, Utah.....	Do.....	12	25	75	0	0	0	92	8	0	0
Stony Lake, Mich.....	Present.....	19	100	0	0	0	0	100	0	0	0
Cold Spring Harbor, N. Y.....	Do.....	202	100	0	0	0	0	100	0	0	0
Tepepam, Mexico.....	Do.....	200	100	0	1	0	0	99	0	0	0
Total.....		7,824	89	11	1	1—	1—	80	2	8	8

Fig. 15 shows the variation in the pattern in the San Francisco Bay region.

Subspecies of the mountains and high latitudes has a larger percentage of the characteristics of $\frac{1}{2} + 3$, $\frac{1}{2} + 3 + 1$, $4 + 5$, and the absence of pronotal dashes and reduction of the light margin in the pronotum.



FIG. 15.—Variation in color-pattern of head of *Hippodamia convergens*. *c* = mode; *a* to *e*, from California.

Subspecies of California, outside of the mountains and humid coast region, is characterized by a large percentage of spotless elytra and of pronota without dashes, and also of a reduction of the white margin. When the basal band is present it is of the variety *extensa* without the other spots.

Subspecies of Western Oregon, except the humid region, has elytra as in California, but the pronota with large dashes which sometimes open to the margin and with the light margins well developed.

Subspecies of the Great Plains shows in many specimens a reduction in the number and size of spots, occasionally entire absence of spots.

Subspecies of the Mississippi Valley, with Missouri as a center, comprise the only specimens of the variety *quindecimmaculata* and its forms (with the exception of two very rare specimens from the Pacific States).

Subspecies of the humid Pacific coast comprises the variety *moesta*. I have seen none of the lighter varieties in collections from the regions where the variety *moesta* is most abundant, but this does not establish their presence or absence.

One large lot taken from the top of Marsh Hill, Fairfield, Washington, contained 15,415 individuals of this species and its different varieties, and 759 individuals of *H. spuria* and its varieties. The various patterns of the *H. convergens* series were sorted and are represented in fig. 16. Those with no spots or with some spots absent but with no confluence are included in the 6,954 individuals of the normal pattern, as it is not feasible to represent the combination of spots present in the figure. They are discussed on a later page.

The march toward greater pigmentation is orderly and determinate, but is not along one definite line of succession. The increase shows itself first generally in the confluence of 4 and 5 or 2 and 3. Whichever appears first, it is generally followed by the other. The coalescence of 1 and 3 is usually the next step. Further pigmentation enlarges these areas to a condition approaching that *H. bowditchi*. Only rarely does pigmentation go to the extent of confluence between $4 + 5$ and 6 or between $4 + 5$ and 2.

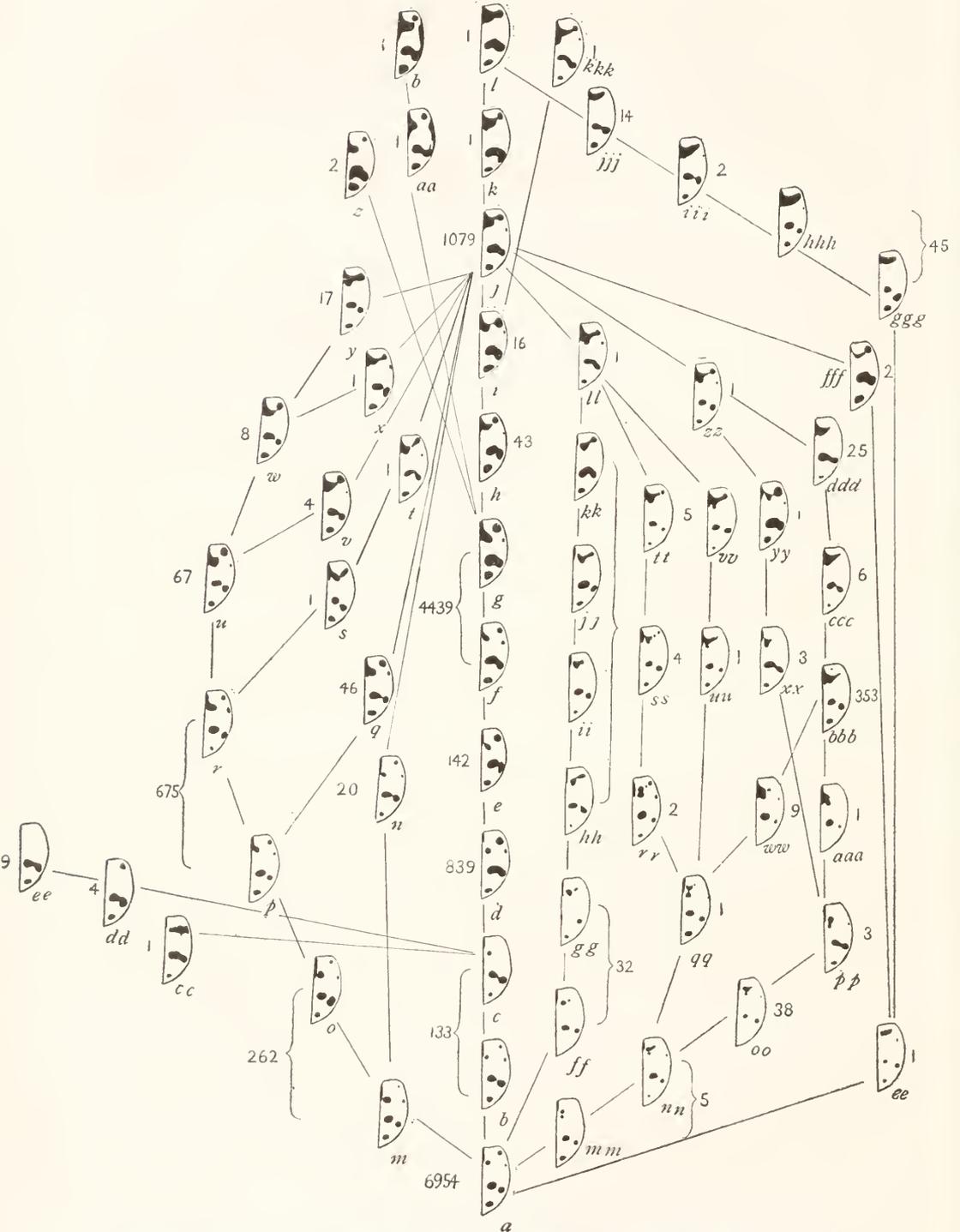


FIG. 16.—Variation in elytral pattern in *Hippodamia convergens* in a hibernating mass of 15,415 individuals from the top of Marsh Hill, Fairfield, Washington.

Quite a different line of development is occasioned by the appearance of spot *e*, the crescent-shaped mark just cephalad of 3 (fig. 16, *nn*, *vv*, etc.). This is the essential feature in the variety *extensa*, but may be seen with various patterns so far as the rest of the elytron is concerned. Ordinarily pigmentation not only makes spot *e* confluent with spot 3, but is so profuse as to hide spot *e* entirely (fig. 16, *zz*). For this reason I am uncertain whether spot *e* is invariably present in the true variety *quinquesignata*. I suspect it is a necessary character, without which 1 and 3 would fail to coalesce or coalesce only as in Nos. 421 and 427. Where $\frac{1}{2}$ is confluent with 3, *e* is often present, but there are cases where it is clearly not present and others where its presence is doubtful. Where *e* is present and pigmentation increases, confluence with 1 may result to form variety *quinquesignata* (*fff*). If 1 is absent, the pigment projects laterad to an acute angle (*uu*), the condition given the name *extensa* by Mulsant when other spots are absent.

Still another line of development is dependent on the appearance of another new spot which I call *q*, just laterad of spot 3 (*ff*). It is very rare that where *q* is present it is not so widely confluent with 3 as to cause the impression that spot 3 is simply produced laterad (*ii*). Such was my original conception. Another spot, *q'*, may carry the pigment still farther laterad. It may even coalesce with 2, but the tendency is not a strong one, for the pigment frequently stops short of it, with a narrow line of the ground-color intervening.

Confluence of *q* with $\frac{1}{2}$ and of *q* and *q'* with 1 is seen very rarely. Spots 4 and 5 are generally larger when *q* is present, and 4 is frequently squarish in outline. This makes it possible that we have in variety *quindecimmaculata* and its allied varieties a distinct species, although that view is not here adopted.

Spotless elytra are most frequent in the non-mountainous and non-humid sections of the Pacific States. Specimens from Onaga, Kansas, sent me by Mr. Crevecoeur, show the absence of several spots. Reduced pigment is also known from Phoenix, Arizona, and Black Hills, South Dakota. I suspect the specimens from the Black Hills were obtained from the plains around the Black Hills rather than from their higher portions, as we have the mountainous varieties also reported from the Black Hills. Apparently the Pacific Coast area of the variety *obsoleta* extends through Arizona to the Great Plains, where it exhibits itself more largely in transitional individuals.

TABLE 7.—Number of spots in *Hippodamia convergens*.

Locality.	No.	0	1	2	3	4	5	9
		<i>P. ct.</i>						
Kamaick Butte, Wash.....	15,415	0.06	0.20	1.08	3.64	8.62	27.3	59.2
Palo Alto, Cal.....	1,033	.29	.78	1.46	.78	.87	22.3	93.9
Cold Spring Harbor, N. Y..	202	0	0	0	0	0	1—	99+

The variation of the number of spots is shown in table 7. At Palo Alto (data from Kellogg and Bell, 1904) and at Cold Spring Harbor the polygons are not regular, but show a normal condition of 6 spots, with a scattering few having aberrant numbers. I have grouped 25 specimens, said by Kellogg and Bell to have 1 or more extra spots on one or both sides, with those having 6 spots, because the irregular position of these spots and my experience with living specimens makes me believe that such spots are nearly always, except when at *e* and *q*, of ontogenetic origin. The poly-

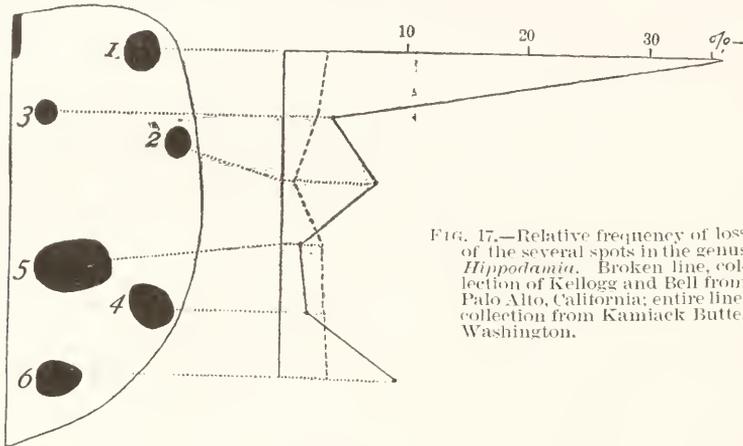


FIG. 17.—Relative frequency of loss of the several spots in the genus *Hippodamia*. Broken line, collection of Kellogg and Bell from Palo Alto, California; entire line, collection from Kamiack Butte, Washington.

gon for Kamiack Butte might have shown about 0.5 per cent, with a seventh spot *e*, but I have not put these in, because no accurate account can be made of spot *e*, as it may be entirely covered with pigment from spot 3 and the scutellar mark. Now, in contrast to the condition at Palo Alto and Cold Spring Harbor, we have at Kamiack Butte a polygon not greatly unlike the half-Galton curves found in some petal-counts. Yet the real nature of the variation in the three cases must be the same. Such an instance shows us that the distinction between continuous and discontinuous variation is not a sharp one.

The order in which the spots disappear has proved to be a matter of great interest. I have tabulated the data given by Kellogg and Bell (1904) Palo Alto, California, in table 8, and fig. 17 (broken line), but have numbered the spots according to Weise. There is no very pronounced order of disappearance here, the most prominent feature being the persistence of spot 2. But at Kamiack Butte (table 8, fig. 17), a very different condition prevails. Here spot 1 exhibits a strong tendency towards disappearance, and this happens in spite of the fact that it is in company with several varieties having spot 1 unusually large and in some cases confluent with spot 3. Spot 6 follows it in order of non-development and then spot 2, which at Palo Alto was most persistent. It is evident, then, that not only is there a definite order, but that this differs from place to place. The

The confluence of spots 5 and 6 is an independent variation. The specimen that Major Casey has from Sonoma County, California, and the one I have from Stony Lake, Michigan, are well marked. It is very rare, without intergrading conditions, and constitutes a distinct position of organic stability.

TABLE 8.—*Spots lacking in Hippodamia convergens.*

[Percentage of beetles in which each spot is lacking.]

Locality.	No.	Spot 1.	Spot 2.	Spot 3.	Spot 4.	Spot 5.	Spot 6.
Palo Alto, Cal.....	1,033	3.5	0.9	2.7	3.5	3.4	3.9
Kamick Butte, Wash.....	15,415	36.2	7.7	4.1	2.4	1.5	9.3
Cold Spring Harbor, N. Y.....	202	0	0	0	0	0	—1
Tepepam, Mexico.....	200	110	7.0	7.0	12.0	13.0	19.0

The loss of the pronotal dashes (fig. 14) and the extension of the black pigment on the pronotum is well marked in specimens from California. Strangely enough, they affect the spotless beetles most. One might conclude that the result is compensatory for the lack of pigment in the elytra, but in Oregon, where spotted elytra are found, the black pattern of the pronotum is reduced, as shown in fig. 14, *a* to *e*. There are probably, therefore, two different causes for the reduction of pigment in the pronota and in the elytra. The only case of an opening of the pronotal dashes (fig. 14) to the margin laterad without communication cephalad was at Fairfield, where the forward opening is not nearly as common as in Oregon. Apparently the line of development is different in eastern Washington from that of western Oregon.

TABLE 9.—*Combinations of spots present and absent in H. convergens from Fairfield, Wash.*

Total.	Present.						Spots.	Absent.						Total.	P. ct. of sum of totals.
	In sixes.	In fives.	In fours.	In trios.	In pairs.	Singly.		Singly.	In pairs.	In trios.	In fours.	In fives.	In sixes.		
9,828	9,121	615	69	13	10	0	1	3,583	1,258	548	156	32	10	5,587	36.2
11,779	9,121	4,166	1,131	283	69	9	3	32	196	278	97	23	10	636	4.1
11,233	9,121	3,871	975	219	11	3	2	327	352	342	122	29	10	1,182	7.7
15,191	9,121	1,191	1,247	512	107	13	5	7	80	49	59	19	10	224	1.5
15,048	9,121	4,190	1,265	387	80	5	1	8	62	171	86	27	10	367	2.4
13,992	9,121	3,957	621	269	22	2	6	211	706	292	144	30	10	1,423	9.3
Av.	9,121	3,498.3	884.7	280.5	55.3	5.3	699.7	412.3	280.5	110.7	26.7	10	9,419	10.2

CORRELATION.

The correlation between the confluence of spots 4 and 5 with the confluence of spot 3 and the mark $\frac{1}{2}$ is represented in table 10, and of 4 and 5 with the confluence of 1 and 3 in table 11. These tables show that the correlation falls far short of the current notion, expressed in the systematic literature, that these confluences are definitely coupled.

An examination of table 6 shows that where black spots on the elytra are absent the pronotal dashes are also absent in a large number of cases

in some California localities, but not in others. At Coolidge, New Mexico, where spots are confluent, the pronotal dashes are absent in a large proportion of cases and are present where there is no confluence. This is also noticeable in some small lots from Colorado and Utah, but in the Pacific States this difference is not marked.

TABLE 10.—Correlation of relation of spots ½ and 3 with relation of spots 4 and 5 in *Hippodamia convergens* at Fairfield, Washington.

Relation, ½ and 3.	4 and 5.				
	Confluent.	Transition.	Separate.	Absent.	Total.
Confluent.....	* 177	2	22	1	202
Transition.....	1	0	6	1	8
Separate.....	11	1	† 99	4	115
Absent.....	0	0	5	‡ 1	6
Total.....	192	3	132	7	334

* *Quindecimsignata* and *caseyi*. † *Convergens*. ‡ Var. *obsolata*.

TABLE 11.—Correlation of relation of spots 1 and 3 with relation of spots 4 and 5 in *Hippodamia convergens* at Fairfield, Washington.

Relation, 1 and 3.	4 and 5.				
	Fused.	Transition.	Separate.	Absent.	Total.
Fused.....	* 64	0	0	0	64
Transition.....	1	0	0	0	1
Separate.....	† 120	3	‡ 59	0	182
Absent.....	7	0	74	‡ 6	87
Total.....	192	3	133	6	334

* Var. *quinquesignata*. † Var. *caseyi*. ‡ *Convergens*. § Var. *obsolata*.

The lateral extension of the black area on the pronotum to the margin, so as to make "margin incomplete laterad," is associated, strangely enough, with both spotless elytra and elytra with spots confluent. We shall see later that this characteristic is subject to modification, so that the great variation between the several localities in eastern Washington which differ in altitude is readily understood. In fact, a lot of hibernating beetles from Fairfield in 1907 showed far fewer specimens with the margin incomplete laterad than those of another year.

The cephalic extension of the black area of the pronotum causing an incomplete margin cephalad is only common in California and New Mexico with beetles lacking the pronotal dashes, but that it is not a necessary consequence of the absence of the dash is shown by the specimens from Milford, Utah.

We have, then, in different localities, a difference in the correlation and the order of development of the pronotum and the elytra.

MEASUREMENTS.

I have measured, by means of the eye-piece micrometer, the degree of separateness or confluence of the several spots in a lot of beetles from Fairfield, Washington. Fig. 19 gives the result in the case of spots 4 and 5. The micrometer units of 0.625 mm. have been used without change to avoid the introduction of errors of reduction. In order to avoid errors of combinations the original classes are used, even though it makes the polygons somewhat irregular. The reader may make his own combination of classes mentally. Of course, since it was necessary to measure a projection of the curved surface and as the distance measured was not always at the same focal distance, there are errors involved. Experimental testing, however, shows that the errors are too slight to affect the significant features of the

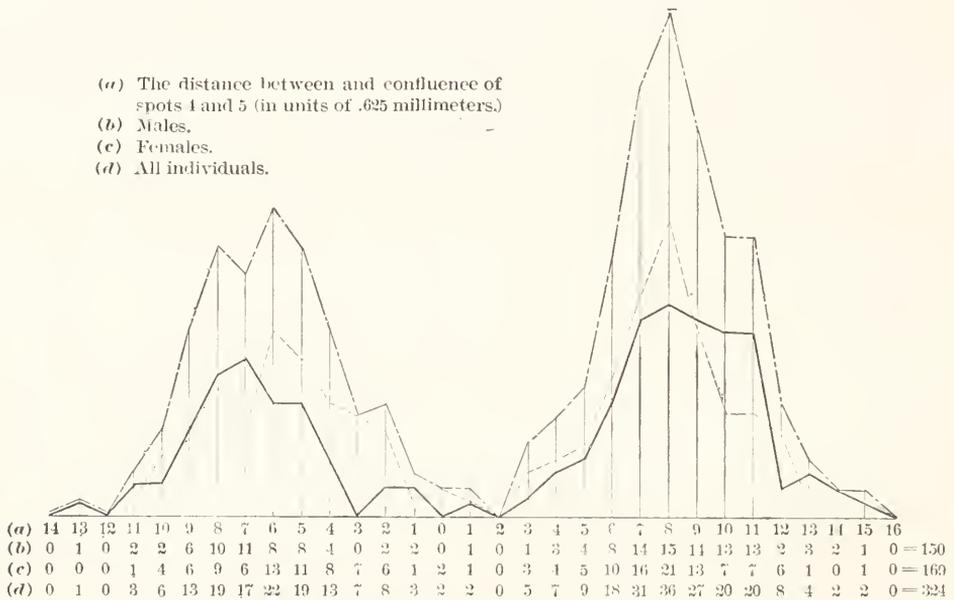


FIG. 19.—Variation of the distance between and confluence of spots 4 and 5 in *Hippodamia convergens* at Fairfield, Washington.

polygons. A novel method has been used in the construction of the curves. 0 is the case where the spots are separated by a distance less than 0.5 unit or confluent to the extent of having a connecting strand less than 0.5 unit in thickness. Increase of distance between the two spots is plotted to the left. Increase in breadth of the connecting strand pigment is plotted to the right.

It will be noticed that the sexes do not materially differ; that the distance apart is more variable than the thickness of the connecting band; that the polygon is bimodal; and that the transitional cases fall for the most part into one or the other of the two polygons.

The variability in diameter of spot 1, shown in fig. 22, is a partial explanation of the previous polygon. Here the variety *caseyi* and variety *quinquesignata* include these individuals at or near 15 units, while the typical specimens are at or near 5 units.

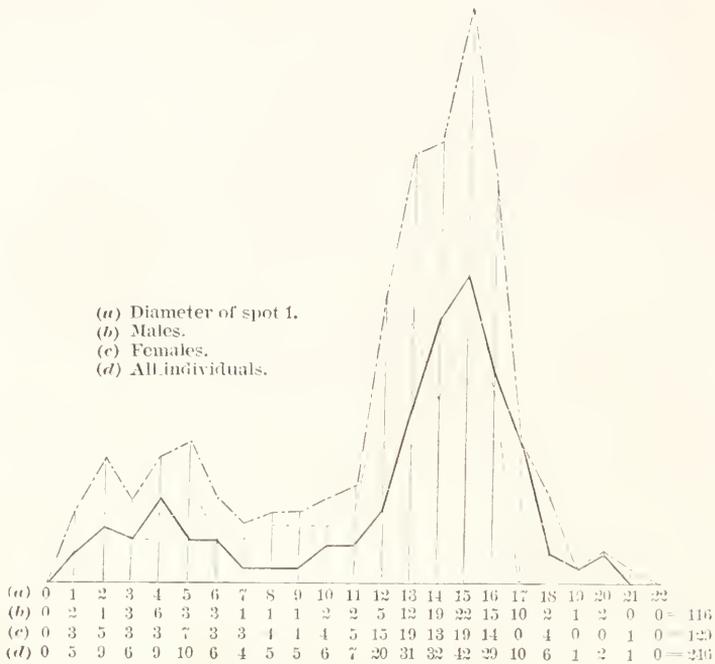


FIG. 22.—Variation in the diameter of spot 1 in *Hippodamia convergens* at Fairfield, Washington.

The variability in diameter of spot 3 is given in fig. 23. Here the typical species is at or near 4 units, and the two varieties just mentioned at or near 8 units. The distance of the lateral edge of spot 3 from the suture is given in fig. 24. The lack of bimodality shows that the extension of pigment laterad in the variety *caseyi* is slight, the main extension being toward the suture in this case. The one individual at 27 units was a case of confluence with spot *c*.

Table 12 was constructed to test the correlation of these color-patterns with differences of size or shape. We see in them that the pronotum is broader in proportion where there is confluence than where there is not.

TABLE 12.—Comparison of ratio of breadth of pronotum to length of elytron in a lot of *Hippodamia convergens* from Fairfield, Washington.

Variety.	Male.	Female.
Without confluence of spots....	52.48 ± 0.20	50.71 ± 0.22
Var. <i>caseyi</i>	54.03 ± .43	51.77 ± .23
Var. <i>quinquesignata</i>	54.06 ± .39	52.11 ± .38

MODIFICATION.

Subjection of the prepupa and pupa to an ordinary poultry incubator at 40° C. resulted in no appreciable modification, nor did increase or decrease in humidity. But an increase of pigment was obtained by exposing the prepupa and pupa to the cold of a refrigerator (5° to 15° C.), a cellar (15° to 17° C.), and the intermittent temperature of an ordinary room where the temperature dropped during the winter months from 12° to 18° C. by day to 5° C. at night. The greatest degree of pigmentation resulted in the last case. The result from one experiment, in which the prepupæ of typical *Hippodamia convergens* were subjected to a freezing temperature out of doors for two nights, was the elytral pattern shown in fig. 25, which is much like that of the western mountain beetles. The other cases give the pronotum that is so frequently found in the western beetles, but elytra not corresponding to any known variety. Fig. 26 is a composite drawing, no one beetle showing the same high degree of pigmentation at every point. Some features of this modification pattern show a correspondence to some

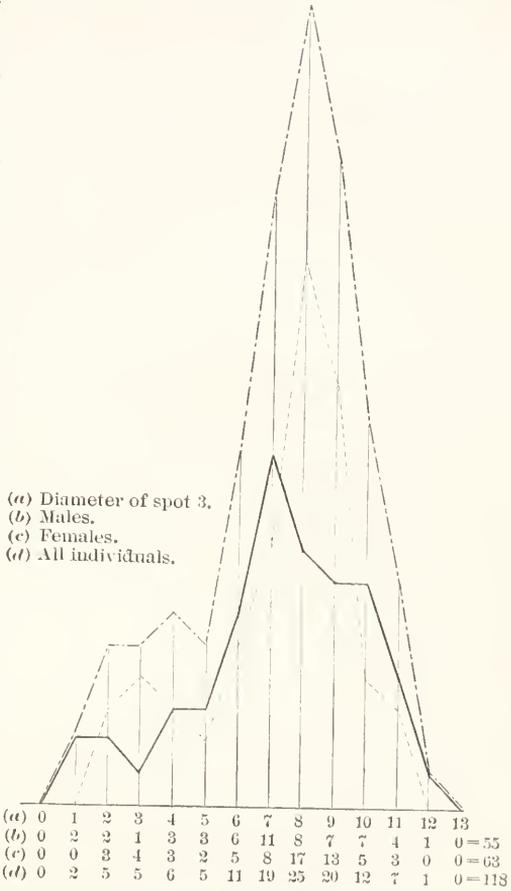


FIG. 23.—Variation of the diameter of spot 2 in *Hippodamia convergens* at Fairfield, Washington.

of the varieties in nature; other features are produced only by artificial modification, especially the pigment line between 1 and 4, which is not the same as the vitta in *Hippodamia spuria* var. or *H. apicalis* var.

HEREDITY.

Every variety or noticeable variation which has been tested is inheritable in some degree. Even though the variety has been brought from a different region, it has maintained itself in our vivarium.

The heredity of spot 1 + 3 shows a nearly perfect segregation. There is a lower degree of segregation in the confluence of 4 and 5. The closest approach to blended inheritance is in the size of the pronotal dash and the incomplete lateral margin of the pronotum. Yet in each of these cases it

is clear that the end positions, that of no spot *versus* spot of normal size in the one case, and lateral margin wholly incomplete *versus* normal in the other case, are more stable conditions; otherwise we should probably have, as a modal condition, a somewhat shorter pronotal dash and a narrower margin, instead of the persistence of a variety in company with a parent species.

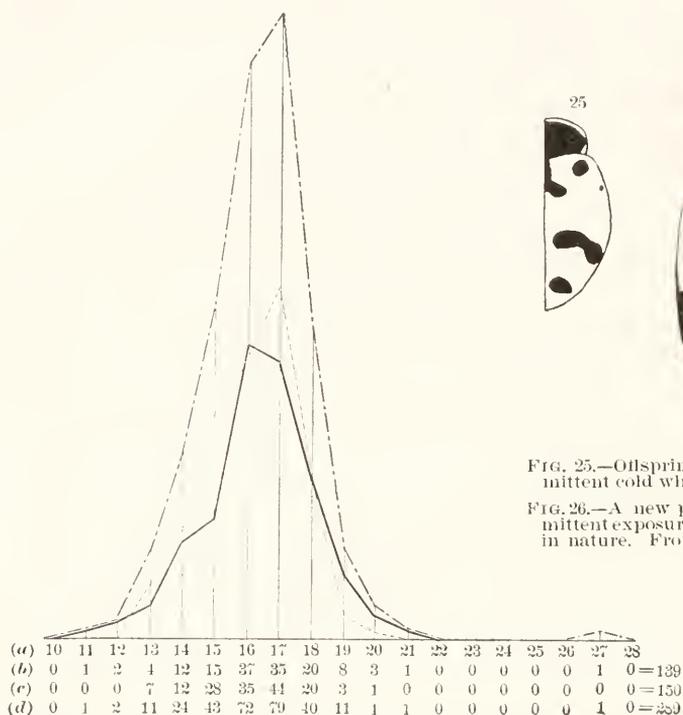


FIG. 24.—Variation of distance from the suture through spot 3 in *Hippodamia convergens* at Fairfield, Washington.

(a) Distance from suture through spot 3. (b) Males. (c) Females.
(d) All individuals.



FIG. 25.—Offspring of 295, exposed to intermittent cold when a prepupa.

FIG. 26.—A new pattern, produced by intermittent exposure to cold, which is not found in nature. From *Hippodamia convergens*.

Owing to the small number of extended pedigrees, the extent of dominance and segregation in these beetles must be examined in large part by the comparison of the numbers in fraternities, only one parent or two parents and one grandparent of which are known, with the theoretical expectations under the several assumptions. In table 13 I have collected, for convenience, the proportions to be expected under the various conditions and assumptions. Thus, if a characteristic gives mixed broods when interbred, it is not recessive, even if the allelomorph is more strongly inherited. It is principally upon this criterion that so many of the pedigrees fail to be simply Mendelian.

Where all the spots are absent (table 15), in the parent, we find this condition ordinarily in the offspring. In the progeny of the 12 females of this kind which had mated in nature, we find that not infrequently a few

of the progeny have a few small spots. None were fully spotted. Combining the progeny of these 12 (81 in all) and weighting small, hazy transitional spots as one-half, we find spots 1 present $\frac{1}{2}$, spot 6 present $5 + \frac{2}{3}$, spot 4 present $9 + \frac{1}{3}$, spot 3 present $8 + \frac{2}{3}$, spot 2 present $11 + \frac{2}{3}$, spot 5 present $16 + \frac{2}{3}$. This higher degree of persistence of spots 2 and 5 and the lower degree of 1 and 6 we have also seen in the variation results in fig. 18. Unfortunately I have no cross of typically spotted and spotless. In 149 we have spotless \times spots 3 and 5. The progeny showed these spots in $6 + \frac{1}{2}$ and $6 + \frac{2}{3}$, respectively, in the 11 offspring. A spotless individual never gave fully-spotted offspring, nor did fully-spotted individuals ever give spotless offspring. Partly-spotted patterns can not be considered a heterozygous condition, because in one experiment where the parents (387) were 2 partly spotted individuals, the 20 offspring were spotless or partly so. The spots which were present most frequently in the offspring were present in the mother, but the particular degree of spottedness was not stable, for several were wholly spotless and several were provided with more and better spots than the parents. We may conclude that in spottedness \times spotlessness simple Mendelian heredity does not prevail, but that crossing gives an intermediate condition which, while not acting like a heterozygote, is yet unstable and contributes to both conditions.

TABLE 13.—Percentage of progeny to inherit a characteristic on simple Mendelian expectation.

Father.	Characteristic is—				
	Dominant.			Trimorphic.	Recessive.
	Mother <i>A A</i> .	Mother <i>A b</i> .	Mother <i>A A</i> or <i>A b</i> .	Mother <i>x x</i> .	Mother <i>a a</i> .
<i>A A</i>	100	100	100		
<i>A a</i>	100	75	100 or 75		
<i>A A</i> or <i>A b</i>	100	100 or 75	100 or 75		
<i>b b</i>	100	50	100 or 50		
(?).....	100	50 to 100	100 to 50		
<i>x x</i>				100	
<i>x y</i>				50 with 50 inter.	
<i>y y</i>				100 inter.	
<i>a a</i>					100
<i>B B</i>					0
<i>a B</i>					50
<i>A A</i> or <i>a A</i>					0 or 50
(?).....					0, 50, or 100

Spots 1, 2, and 6 are often solely absent in regions where spotlessness prevails, so that their individual heredity becomes of interest. Spot 6 was not lacking in any of the offspring of No. 228 ♀, which was so characterized, but of the similar No. 232 ♀ the single offspring had the spot reduced. In No. 455, where 6 was transitional, it was normal in all the offspring.

The presence of this spot is, then, either dominant or preponderant over its absence.

Spot 2 was also either dominant or preponderant, for where the mates were opposed in this character, presence of the spot in the offspring always prevailed. Inheritance of spot 1 was studied in material from Fairfield, Washington, where it is frequently lacking. Its presence is less strongly inherited than that of the other spots, being found in less than half of the progeny in the case of presence \times absence. I believe that this result has a connection with the fact of its frequent absence in that locality. This is in contrast to the inheritance of spots 2 and 6.

The size of spots is inheritable, as seen in fig. 27, where the unusual proportion in size between 4 and 5 is inherited in some degree. This is conspicuously true of the size of spot 1, where we have, besides the normal center of variation, a second, made up of varieties *quinquesignata* and *caseyi*, having the spot large. The shape of spots is also inheritable; thus in fig. 27 the influence of 4 + 6 in one of the parents shows itself in the progeny, though they lack that confluence.

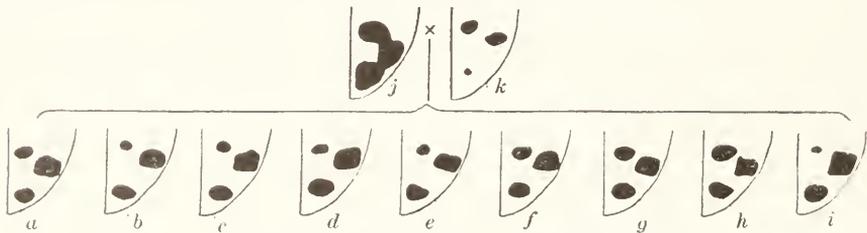


FIG. 27.—Elytral pattern of offspring of 259.

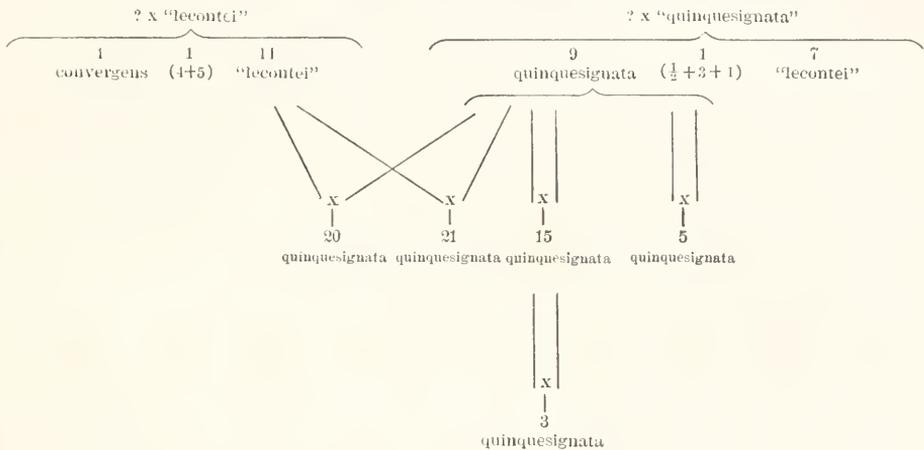
The confluence of 4 and 5 is regularly inherited in the heavily pigmented individuals, especially in the variety *quinquesignata*. In more lightly pigmented individuals its inheritance is more irregular. It acts as neither a simple dominant nor recessive, yet segregation is evident. The suggestion that a greater degree of pigment is always dominant over a lesser degree does not receive support.

The confluence of 4 and 6 has neither dominance nor trimorphic heredity. It is segregate,* however, and apparently subponderant. The confluence of $\frac{1}{2}$ and 3 is inheritable in various degrees, dependent largely upon the degree of its development. There is segregation with some intermediates, yet the suppositions of dominance or trimorphic inheritance are not tenable. The presence of the *extensa* character is difficult of analysis, for its presence may be cloaked with excessive pigment. Yet, bearing this in mind, we see that while there is segregation with some intermediates, neither dominance nor trimorphic heredity are found.

*The expression "alternative heredity" is a misnomer in cases where the heterozygotes are intermediate and I therefore prefer the term "segregate heredity." This is divided into amphimorphic heredity, where the two parental conditions are represented in F_2 , and trimorphic, where, in addition, we have a third intermediate condition in F_2 .

All cases of the confluence of 1 and 3 are not inherited alike. In matings of No. 421 ♀ and No. 427 ♀, the confluence is the result of the overgrowth of 1 and 3. There is no mutual projection of the spots and they are not confluent when the spots first appear in ontogeny. Such cases of confluence are not inherited in kind, because, being only extreme fluctuants, the offspring do not attain their magnitude, and therefore no confluence results. In the cases of true confluence, again, there are two kinds which are inherited differently. In one kind, typified by No. 351 ♀, spot 1 is small, so that the basal band tapers to it without an enlargement. This is rather unstable and its inheritance has many of the irregularities

TABLE 14.—Pedigree table of a race of the variety *quinesignata*.



of the preceding characteristics. In cases of the confluence of 1 and 3, where there is heavy pigmentation with spot 1, showing as a conspicuous enlargement, the variety *quinesignata* (350 ♀, 382 ♀, 390 ♀, and 422 ♀), the inheritance is unique, showing a high degree of stability and segregation. The results (table 15) are not inconsistent with the hypothesis of dominance, but in 382 ♀ and 439 ♀, where we have a transition to confluence of 1 and 3, there are nonconformable results, so that even if there be dominance here it is not firmly established.

Explanation of Table 15.

The letters in the columns headed "Father" and "Offspring of" indicate that the individual was unknown, but must have been from the locality indicated, as follows: B., Berkeley, Cal.; C., Chewelah, Wash.; C. S. H., Cold Spring Harbor, N. Y.; D., Dilley, Oreg.; F., Fairfield, Wash.; O. B., Oyster Bay, N. Y.; P. A., Palo Alto, Cal.; R., Redlands, Cal. The prevailing patterns at these localities are given in preceding tables.

F or M in the remaining columns places the father and mother, respectively, in the category named at the head of the column. In other respects it was a typical *H. convergens*. f indicates that the sire was used with a female that was probably already fecundated and hence was improbably the father. These series were included in order that their characteristics might be preserved for subsequent families; but these were rarely obtained.

The numbers under "Father" and "Mother" are designations of the parents; in the remaining columns they indicate the number of offspring in the several categories.

* Indicates that information is lacking as to the character of the pronotal markings.

- (1) Pronotum of M modified by cold. Offspring emerged in autumn.
- (2) Spots 2 and 3 are larger in progeny than in parent, yet are smaller than normal.
- (3) The light basal mark very prominent in M, normal in progeny.
- (4) In M, 4 is very near to 5. Of 3 others subjected to cold 1 had 1 tr. 5.
- (5) In M, 1 + 3 became slightly confluent after several days.

The convergent dashes upon the pronotum were shown by Kellogg and Bell (1904) to vary in size down to absence, and my observations confirm this. No high degree of segregation is expected, then, in inheritance, and none is found. Where the parents have intermediate dashes, the progeny also have, although some may be just large enough not to be classed as small in the table. The inheritance, then, is blending, but with so high a variability that both absence and a considerable size may occur in one fraternity.

The condition of pronotal dashes communicating with the light margin is inherited in an average of 27 per cent, when the one only known parent has the characteristic. Where the other parent does not have it, as with 149 ♀, none of the offspring have such a communication. Where both parents have the communication, as in 435, then 6.5 in 11 possessed it. There is, therefore, neither dominance nor trimorphic heredity, but subponderance.

The data upon the incomplete margin cephalad is only adequate to show that this character is inheritable and shows some segregation. The incomplete margin laterad is classified upon an unsatisfactory basis, since so many individuals have the margin almost incomplete. We have furthermore to deal with some modification. Yet it is clear that the characteristic is inherited in part and it seems to give us continuous variation. It is quite possible that intermediate degrees are discriminated against in development and that either a large lateral projection or a very slight one is favored, as the facts of variation and distribution would cause us to suspect.

If this species as here constituted is ever to be dismembered, it is most probable (aside from the removal of variety *moesta*) that variety *quinquesignata* and variety *caseyi* will be removed as *H. quinquesignata*. There is some ground for this step, although, considering everything, I have not chosen to make it. My experiments show a partial intersterility between specimens of variety *caseyi* of full pigmentation and eastern specimens of *H. convergens*. But there was interfertility between specimens with the same confluence in a lesser degree and having spot 1 small (the variety *defecta*) and eastern specimens of *H. convergens*. I have only hesitated from the division because I do not know whether variety *caseyi* and variety *defecta* may not be interfertile. The presence of intergrades causes me to suspect that this is not only so, but that they habitually interbreed. At any rate, this seems to be a point at which this species may in the future divide to give us two species, even though it may not yet have done so.

3036 a. *Hippodamia bowditchi*, new species.

Distribution: Northern Rocky Mountains.

The type (fig. 28, *d*) and 5 cotypes (fig. 28, *b*, *c*, *e*, *f*, *g*) of this species were collected from goldenrod August 12, 1904, on the bank of the river at St. Maries, Idaho. The pattern is comparable to that of *H. convergens* and variety *quinquesignata* and would be considered a variety of that species but for the distinct hiatus between the 4 specimens of variety *quinquesignata* and 11 of other varieties of *H. convergens*, taken in the same lot, on the one hand, and the 6 in question on the other hand. The black bands of *quinquesignata* are here much enlarged; the intermediate band is thicker in the baso-apical direction than the space between it and the basal band. The wide basal band is nearly uniform in width and thus shows little evidence of its component spots. It shows no rounded projection at the position of spot 3. Spot 2 is absent and the apical spot is much enlarged. The intermediate band is so enlarged as to obscure its compound nature and its apical margin shows no angulation. Its basal margin has an angulation, but no restriction is produced in the band. The band extends far toward both the suture and the costal margin and shows a straightened edge in these directions.

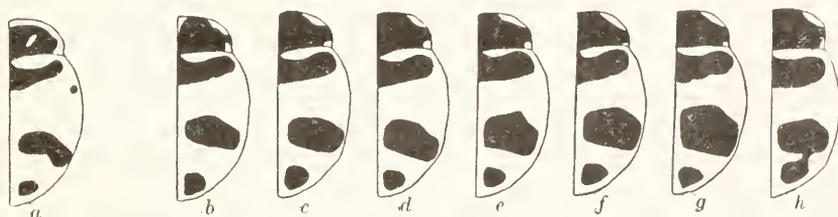


FIG. 28.—Variation of color-pattern of *Hippodamia bowditchi*. *d* = mode; *b* to *g*, from St. Maries, Idaho; *h*, from Bitterroot Mountains; *a*, a specimen of *H. convergens* var. *quinquesignata* collected with them.

With the exception of a very slight convergent dash on one side of one specimen (fig. 28, *a*) the pronotum is spotless. The black pattern reaches the cephalic border of the pronotum on each side and in some cases extends along it for some distance (fig. 28, *d*). The black pattern always shows a lateral extension which generally reaches the border and in some cases extends to the caudo-lateral corner (fig. 28, *b*). The variation of the pronotum is paralleled by individuals of *H. convergens*.

The ground-color is yellow without a trace of reddish color, in strong contrast with that of the accompanying specimens of *H. convergens*. The peculiar ground-color suggests the possibility that these beetles are only larvæ of *H. convergens* modified by some unusual food. Such an hypothesis must be rejected for the present for the more likely one of a specific difference. Unfortunately, I have been unable to attempt hybridization between this new species and *H. convergens*.

A specimen from Kalispell, Montana, and one from between Hope and Okanogan, British Columbia, in the collection of Mr. F. K. Bowditch, belong here. A specimen in the Museum of Comparative Zoology from the Bitterroot Mountains has the characteristics of this species and, in addition, a slight confluence of 4 + 5 and 6 which is subordinate to the extreme confluence of 4 + 5. Further collections in these mountains adjoining the type locality might give us in this species a still further development in this direction.

3047. *Hippodamia spuria* Leconte.

Distribution: Plateau and Pacific States and British Columbia.

This is a variable species (fig. 29), but the forms show little geographical differentiation. *H. sinuata* and *cockerelli* are specifically distinct derivatives, so far as our present knowledge goes.

Typical pattern (fig. 29, a): Suture not black, except at basal quarter. Spots 1, 4, 5, 6. 256 individuals in 759 = 34 per cent, at Fairfield, Washington.

Var. *lineata* (n. var.).

The scutellar spot is replaced by a black suture only slightly wider at one-quarter. Intergrades occur, but they are less common than the variety. This character is found in conjunction with most of the varieties of elytral pattern; 3 in 759 with 2 transitional, at Fairfield, Washington.

Var. *a*.

Spots 1, 4 + 5, 6. 447 in 759 = 59 per cent, at Fairfield, Washington (fig. 29, h).

Var. *β*.

Spots 1, 5 + 4 + 6. 37 in 759 = 5 per cent, at Fairfield, Washington (fig. 29, k).

Var. *complex* Casey.

1 + 4 + 5 + 6. Scutellar mark short. Not at Fairfield, Washington; Vancouver Island (fig. 29, j).

Var. *crotschi* Casey.

1 + 4 + 5, 6. Scutellar mark short. 12 in 759 = 2 per cent, at Fairfield, Washington (fig. 29, i).

Var. *γ*.

Spots 1, 4 + 5 + 6. Rare, Idaho. Nowhere established (fig. 29, n).

Var. *ε*.

Spots 1 absent, 4, 5, and 6 reduced. 2 in 759 at Fairfield, Washington; Colorado (fig. 29, q).

Subspecies of Colorado: Reduction is most manifest in Colorado, a parallel to the condition in *Hippodamia apicalis* in Colorado. Whether it is local to some part of Colorado, as is probable, or not, can not be told because of the former pernicious habit of labeling by States only.

The confluence manifests itself in each individual either as 1 + 4 + 5 or 5 + 4 + 6, and never at Fairfield involving all 4 spots even in a slight degree. The two varieties are therefore distinct in this locality. In Vancouver Island, however, the combination is found.

The pronotum is much less frequently subject than that of *H. convergens* (see fig. 30) to a reduction of pigment in such a way that the convergent light mark is confluent with the light margin. This was found in

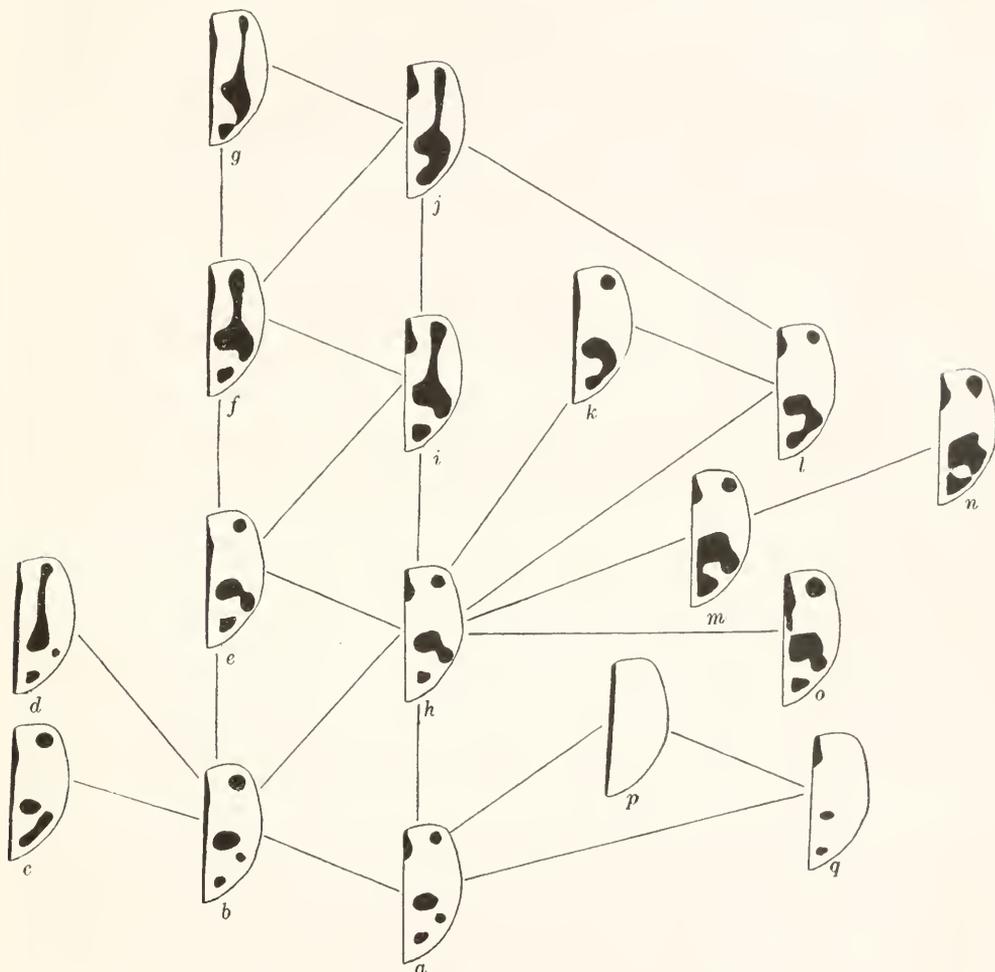


FIG. 29.—Variation of elytral pattern in *Hippodamia spuria*.



FIG. 30.—Variation of pronotal pattern in *Hippodamia spuria*. Mode = c to s.

FIG. 31.—Variation of head-pattern of *Hippodamia spuria* from Dilley, Oregon. b = mode.

only 5 in 759 at Fairfield. On the other hand, there was one specimen in the Fairfield lot in which the convergent mark extended to the caudal margin of the pronotum and another in which it very nearly did so. In each of

these cases the pronotum was lacking pigment at an independent center—the caudal margin of the pronotum. The variation of the color-pattern of the head is given in fig. 31.

HEREDITY.

Table 16 epitomizes the results of the heredity experiments with respect to the elytral pattern. No. 368 ♀ has a pronotum with pronotal dashes open to the margin cephalad. None of the 18 offspring possess the characteristic. Since the same characteristic is inherited in *H. convergens* (375 ♀), it is probable that its lack in the offspring here is the result of recessiveness or subponderance.

TABLE 16.—Heredity in *Hippodamia spuria*.

[For description of form of table and abbreviations see table 15, pp. 42, 43.]

Father.		Mother.		Sutural pigment.			1 and 5.			1 and 5.			5 and 6.					
No.	Offspring of—	No.	Offspring of—	No.	Short.	Intermediate.	Long	Separate.	Approach	Transition.	±	Separate.	Transition.	±	Separate.	Transition.	±	
F	F	368 ♀	F	18	M 17	1	18	M 18	11	4	3
D	D	227 ♀	D	7	M 7	4	M 2	1	M 7	7
262 ♀	227	262 ♀	227	5	F M 5	2	3	F	F M 5	5	
400 ♀	F	400 ♀	F	18	M 18	18	FM 15	I	2	18	
± 9 ♀																		
383 ♀	F	383 ♀	F	23	F M 23	9	F M 11	1	2	F M 23	23	
± 9 ♀																		
461 ♀	383	461 ♀	383	3	F M 3	1	1	F M 1	F M 3	3	
489 ♀	383	489 ♀	400	3	3	F	M	F 3	
380 ♀	F	380 ♀	F	11	F 19	5	M 20	11	F	FM 11	7	26	11	
± 9 ♀																		
437 ♀	380	437 ♀	380	4	F M 4	4	F M 4	4	
412 ♀	380	412 ♀	380	15	F 9	M 5	1	15	F M 5	3	7	15	
445 ♀	380	445 ♀	380	9	4	F M 1	4	9	F M 4	1	4	9	
432 ♀	380	432 ♀	380	12	6	F M 5	12	1	F 3	M 8	12	
433 ♀	380	433 ♀	380	5	2	1	F M 2	5	F M 5	5	

In the elytral pattern the table shows that the sutural mark is inherited segregately, with some intergradation. We have two centers of variation, but not two unit-characters. The long sutural mark is neither recessive nor dominant, nor is there any regular dominance in the relation of spots 4 and 5. There seems to be a preponderance of short sutural pigment and of 4 + 5, which are more common than the opposed conditions.

3048. *Hippodamia oregonensis* Crotch.

Distribution: Cascade Mountains.

Although the pattern of this species (see fig. 32) is parallel to that of *H. convergens* var. *quinesignata*, a collection of the 2 from Pinnacle Peak, Washington, shows a difference in form of body and shape of the spots. This makes it probable that it has been derived from *H. spuria* by the addition of the banding character. The possible influence of

the mountain environment will later be discussed in this connection. The vittate tendency is much more marked here, as might be expected, than in *H. convergens* var. *quinqesignata*, nearly all specimens showing some evidence of it. The absence of pronotal spots is another result to be expected from the mountain environment.

The basal band is the chief differential from *H. spuria*. Specimens of that species differing only by absence of pronotal dashes are often labeled *H. oregonensis*. Such specimens should be considered a variety of *H. spuria*, as presence or absence of pronotal spots alone is a character of less distinction in *Hippodamia* than presence or absence of the basal band.

Form *a*. Spots $\frac{1}{2}+1$, 6+4+5, Pinnacle Peak, Washington.

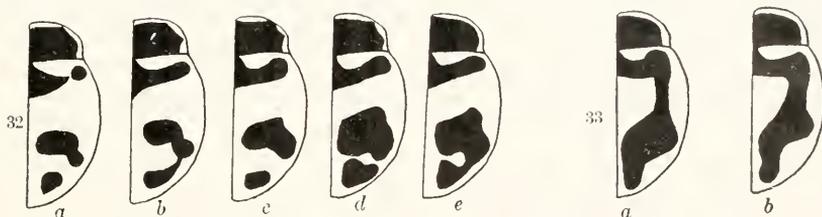


FIG. 32.—Variation in color-pattern in *H. oregonensis*. *c* = mode; *b*, from Oregon; *c* to *e*, from Pinnacle Peak, Washington.

FIG. 33.—Variation in color-pattern of *H. cockerelli*. *a*, from Colorado; *b*, from Yellowstone Park.

3048 a. *Hippodamia cockerelli*, new species.

Distribution: Colorado to Wyoming.

This species resembles *H. spuria*, except in color-pattern (see fig. 33). This is remarkable in possessing vittæ and banding in combination. It is the Rocky Mountain equivalent of *H. oregonensis* of the Cascade Mountains. The two mountain systems have given two different mountain species derived from *H. spuria*. If intergrades are ever found it will probably be at the convergence of the two mountain systems in British Columbia. The type is in the U. S. National Museum. It was collected by Prof. T. D. A. Cockerell, in honor of whom the species is named, in Cottonwood Gulch, on the west slope of the Sangre de Christo Range, in the Hudsonian Zone, in Saguache County, Colorado, August 4, 1887.

There are also two specimens from Yellowstone Park in the collection of Mr. F. P. Bowditch. The three show very little variation. I have never seen any tendency to the formation of a basal band in *H. spuria*, although I have seen many specimens in the Western States. This species has apparently arisen discontinuously. The complete lack of intergrades I have taken to indicate that it is intersterile with *H. spuria*, since complete dominance, even if there be complete segregation, is not to be expected in coccinellid color-patterns.

3046 b. *Hippodamia dispar* Casey.

Distribution: Colorado.

Of this very rare species I have seen only the type in Major Casey's collection, the specimen in the U. S. National Museum, and the one in the Leng collection (fig. 34). The 3 specimens show some variation in the rotundity of 4+5, but the combined spot is in all cases much rounded. The rounded enlargement of the 4+5 area in *H. cockerelli* points strongly to a derivation of *H. dispar* from *H. cockerelli*. A large series might reveal an amount of intergradation which would bring them into one species. But at present the few specimens known are distinct.

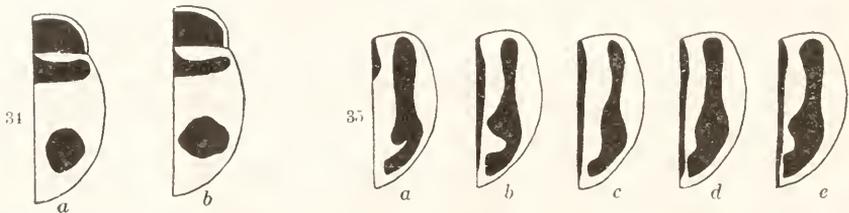


FIG. 34.—Color-pattern of *H. dispar* from Colorado.

FIG. 35.—Variation of elytral pattern in *H. sinuata*. *b*—mode; *b* to *e*, from Alameda, California; *a*, variety *crotchii*.

3049. *Hippodamia sinuata* Mulsant.

Mulsant's description seems to apply to the same beetles later named *H. trivittata* by Major Casey, and his type came from the same locality. This Californian species (see fig. 35), with the vittæ complete, is, however, distinct from the other beetles often called *H. sinuata*, which have the vittæ very strongly bowed in the apical half of the elytra, or incomplete or lacking; these latter are properly placed in *H. spuria*.

Mr. Nunenmacher informs me that *H. sinuata* is restricted to the salt-marshes, and in my collection in California I failed to find them outside of the marshes. It is this fact, together with the lack of intergrades, that causes me to consider them specifically distinct. This isolation by its decrease of interbreeding would have afforded the opportunity to establish intersterility.

Var. *crotchii*.

The suture black for only one-third of the length. One specimen from San Francisco in the collection of Mr. Leng.

3050. *Hippodamia tredecimpunctata* Linnæus.

Distribution: Europe, United States, and Canada.

This species is the least variable of all the widely ranging species of *Hippodamia*. Yet large series show variation (see figs. 36 to 38). This is parallel in part to that given for Europe by Weise (1899) and Mulsant (1846). The names and letters employed by them will be used. While

some of these varieties as noted have not yet been found in America, most of them are to be expected.

Var. *padana* Weise. Black pattern on pronotum small, less than twice the width of the light margin (cf. fig. 37). Elytral spots small.

Var. *signata* Faldermann. Black pronotal pattern narrow. Elytra spotless. One from Washington, but with mark $\frac{1}{2}$.

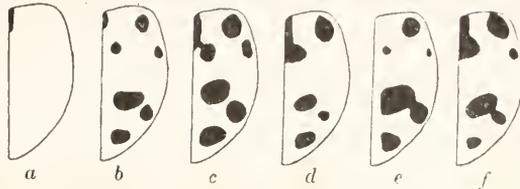


FIG. 36.—Variation in elytral pattern in *H. tredceimpunctata*. *b* = mode; *a*, from Washington; *b*, *c*, from Montana; *d*, from California; *e*, from Massachusetts; *f*, from Oregon.

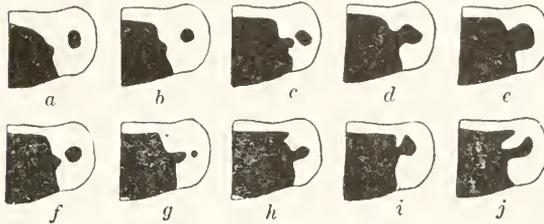


FIG. 37.—Variation of the pronotal pattern of *H. tredceimpunctata*. *d* = mode; *a* to *e*, from Stony Lake, Michigan. *f* to *j*, from Pacific States.



FIG. 38.—Variation of color of head in *H. tredceimpunctata*. *b* = mode; *a* to *d*, from Stony Lake, Michigan; *e*, from California.

Var. *lacta* Weise. Lacks spot 2 and $\frac{1}{2}$.

Var. *undecimmaculata* Harrer. Lacks spot 2.

Var. *scutellaris* Weise = *D* Mulsant. Lacks mark $\frac{1}{2}$.

Var. *triloba* Weise = *F* Mulsant. Spots $3 + \frac{1}{2}$.

Var. *spissa* Weise = *G* Mulsant. Spots $4 + 5$.

Var. *marchica* Weise. Spots $1 + 2$, $4 + 5$, 6. Not seen in America.

Var. *contorta* Weise. Spots 1 , $\frac{1}{2} + 3$, $4 + 5$, 6.

Var. *c-nigrum* Weise = *H* Mulsant. Spots $4 + 5 + 6$ in form of letter *c*.

Var. *gyllenhali* Weise = *I* Mulsant. Spots $\frac{1}{2}$, 1, 2, 3, $4 + 5 + 6$ in the form of a large angular patch. Not seen in America.

Var. *sellata* Weise. Spots $\frac{1}{2} + 3 + 2 + 5$, 1, 6. Pattern saddle-shaped. Not seen in America.

Var. *borealis* Weise. Elytra black with one or two reddish spots. Not seen in America.

Var. *A* Mulsant. The sublateral spot of pronotum confluent with the central pattern (see fig. 37). In a lot of 111 from Stony Lake, Michigan, 80 per cent were of this variety, 10 per cent with a sublateral spot separate, and 10 per cent transitional.

Var. *B* Mulsant. Several of the black spots absent. One from Garland, Colorado.

Var. *E* Mulsant. The mark $\frac{1}{2}$ prolonged to level of spot 3. Rare.

Subspecies of Oregon to California: Specimens from this region show spot $3+\frac{1}{2}$, spot 2 absent, and 4 small. The pronotal pattern has an additional lateral process cephalad of the usual one.

3053. *Hippodamia americana* Crotch.

Distribution: Lake Superior and Hudson Bay.

The type specimen in the Leconte collection makes it clear that this abused name belongs to a species closely allied to *H. tredecimpunctata* rather than to specimens of a variety of *H. spuria*. It is essentially a black-sutured, usually vittate derivative of *H. tredecimpunctata* (fig. 39). The specific rank must be retained for the present because of the lack of a large series. The great variation in the few specimens known makes it possible that larger numbers from Lake Superior might reduce it to a variety of *H. tredecimpunctata*. The pronotum has the pigment so extended that it generally conceals the characteristic lateral projection of *H. tredecimpunctata*.

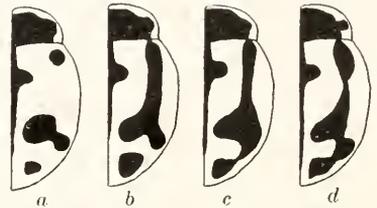


FIG. 39.—Variation in pronotal pattern in *H. americana*. *a*, from Hudson Bay; *d*, from Lake Superior.

3051. *Hippodamia parenthesis* Say.

Distribution: United States, except the southeastern States.

Fitch has named a long series of forms, some of which are scarcely worthy of recognition (see fig. 40). Being based on one character, two or more of these forms are often embodied in one specimen. There is more intergradation in this species than in the others of *Hippodamia*.

Form *tridentifrons* Fitch.

Three white spots on head confluent. Common. (See fig. 41.)

Form *permacrifrons* Fitch.

Three spots on head, separate and reduced.

Form *triangularis* Fitch.

White spot on pronotum, triangular instead of square. Rare. (See fig. 42.)

Form *lituricollis* Fitch.

Black pattern of pronotum much reduced, not touching caudal edge of pronotum and "having a large black dot on each side confluent with it by a neck only one-half as thick as the dot." This form is interesting as showing components of the pattern similar to those in *H. tredecimpunctata*.

Form *albomaculata* Fitch.

White basal spots adjoining scutellar marks.

Form *linearis* Fitch.

The scutellar mark linear, not dilated.

Form *approximata* Fitch.

The humeral spots touch the base of the elytra.

Form *disco-punctata* Fitch.

Spot 5 thick and round instead of oblong.

Form *tridens* Fitch.

Spot 5 separate from 4+6. In many localities this exceeds the type in abundance.

At Stony Lake, Oceana County, Michigan, 29 per cent of 652 have spot 4 separate, 3 per cent transition, and 68 per cent confluent in some degree.

Form *confluenta* Fitch.

Spots 5+4+6. Strongly confluent, only a narrow cleft dividing the mesal ends of 4 and 6.

Form *connata* Fitch.

Spots, 1, 4+5+6 making one large patch.

Form *insulata* Fitch.

Spots, 1, 4+5+6 inclosing a small light spot.

Form *nimia* Fitch.

Spots 1, 3, 4+5+6. Fitch reports 3 in 40 cases. At Stony Lake, Michigan, there were 16 per cent in 657.

Mulsant gives 2 varieties characterized by loss of some spots, but I attribute these to *Hippodamia apicalis*, where the tendency to reduction in a part of its range is strong.

Subspecies of the Eastern States: Characterized by a large percentage of forms *confluenta*, *insulata*, and *connata*.

Subspecies of Oregon: The black pattern upon the pronotum, instead of being only slightly wavy cephalad, has the mesal element strongly projecting on account of the reduction of pigment between it and the lateral element.

Although this species is so widespread, it seems less closely allied to the European members of its subgenus than the much more locally distributed species *H. apicalis* and *H. lengi*.

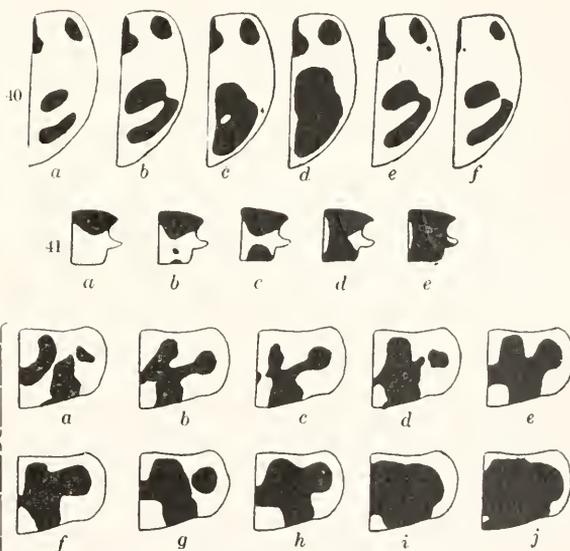


FIG. 40.—Variation in elytral pattern of *H. parenthesis*. *b* = mode; all from Stony Lake, Michigan.

FIG. 41.—Variation of color-pattern of head of *H. parenthesis*. *a*, *b*, from Colorado. Variation of color-pattern of head of *H. parenthesis*. *c* = mode; *e*, *d*, from Stony Lake, Michigan; *e*, from Toronto, Ontario.

FIG. 42.—Variation of pronotal pattern of *H. parenthesis*. *c* = mode; *a* to *e*, from Dilley, Oregon; *f* to *j*, from Stony Lake, Michigan.

3051 a. *Hippodamia apicalis* Casey.

Distribution: Colorado to California, Arizona to Washington.

This species is closely allied to the the previous one (see fig. 43). It is given specific rank because of its smaller size, darker pronotum, different head and elytral pattern, and lack of intergrades. Since its range is within that of *H. parenthesis*, which it does not displace, it can not be a subspecies of it. In the following descriptions, *a* is a black mark along the suture at and near the apex.

Typical pattern: Spots $\frac{1}{2}+3$, 1+2, 4+5+6+ *a*. (Fig. 43, *e*.)

Var. Spots $\frac{1}{2}+3$, 1+2, 6+4+5+6+*a* inclosing a light spot. Arizona. (Fig. 43, *h*.)

Var. Spots $\frac{1}{2}+3$, 1+2+4+5+6+*a* = *H. arctica* Schneider. Nevada and Utah. (Fig. 43, *g*.)

Var. Spots $\frac{1}{2}+3$, 1, 5, 4+6+*a*. Idaho. (Fig. 43, *i*.)

Var. Spots $\frac{1}{2}+3$, 1, 4, 5, 6+*a*. Colorado and Wyoming. (Fig. 43, *c*.)

Var. Spots $\frac{1}{2}+3$, 1, 4, 6+*a*. Colorado and Wyoming.

Var. Spots $\frac{1}{2}+3$, 5, 4+6, *a*. Colorado and Wyoming.

Var. Spots $\frac{1}{2}+3$, 1, 4, 6, *a*. Colorado and Wyoming.

Var. Spots $\frac{1}{2}+3$, 1, 4, *a*. Colorado and Wyoming.

Var. Spots $\frac{1}{2}+3$, 1, *a*. Colorado and Wyoming.

The pronotum is always much darker than in *H. parenthesis*, the caudal white spot being especially reduced. The head has 2 spots near the cephalic border instead of 2 pyramids with their bases upon the border, as in *H. parenthesis*.

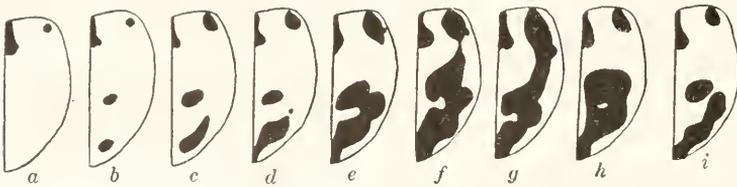


FIG. 43.—Variation of elytral pattern in *H. apicalis*. *e* = mode; *a*, from California; *b*, *d*, from Colorado; *c* from Wyoming; *e*, *f*, *g*, from Nevada; *h*, from Arizona; *i*, from Idaho.

Subspecies of Nevada and Utah: Spots never found missing and the vittate variety frequent.

Subspecies of Colorado and Wyoming: The spots much reduced and some frequently lacking.

Subspecies of Arizona: The black pattern much enlarged but not vittate. A further development in this direction is seen in Southern California in *H. lengi*.

Hippodamia apicalis is more closely allied to the European *H. arctica* and the Siberian *H. amoena* than to *H. parenthesis*, and is, I believe, the American representative of *H. arctica*.

3051 b. *Hippodamia lengi*, new species.

Distribution: Southern California.

In the Ulke collection in the Carnegie Museum at Pittsburg, Pennsylvania, there are 8 beetles which aside from color-pattern resemble *H. apicalis*. They are from California and bear a label—"var. of *H. parenthesis* Horn dix." There is one other of the same kind in the U. S. National Museum from San Diego, California, and one from Southern California in the Horn collection of the Philadelphia Academy of Natural Sciences. These 10 specimens are decidedly different in their color-pattern from all specimens of *H. parenthesis* or *apicalis* that I have seen and should, I believe, be recognized as a species, although it is to be considered as a derivative of *H. apicalis*. I have designated one of the Pittsburg series as the type.

The pronotum is more extensively pigmented than in *H. parenthesis* or *apicalis*. In one specimen the mesocaudal light spot is wholly absent. In the other cases it is small and triangular, with the point caudal. The spots 4, 5, and 6 are confluent, sometimes leaving an inclosed light spot, sometimes with the pigment continuous. The entire suture is pigmented and confluent with the spots just mentioned. The pigment extends laterad in the basal region to spots 1 and 3. The pigment generally involves the base of the elytron, but in one case is free from it.

Var. A. The spot 3 free.

Var. B. The spots 1 and 3 free.

While the amount of confluence at the base of elytron is thus seen to be variable, the distinctive feature of the species, the pigmented suture, is constant. The species is named in honor of Mr. C. W. Leng, student of this genus.

3052. *Hippodamia faicigera* Crotch.

Distribution: Hudson Bay, Great Slave Lake.

The specimens in the Horn and Leconte collections, in addition to their lack of discal spots and to the more elongate elytra, have a lateral margin which is straight or even slightly concave for a short distance. The vittæ are much less sinuate in the apical region than those of *H. sinuata* (see fig. 7). A large series will throw light upon its relationships. For the present we must conclude that it has probably developed along an independent line rather than from *H. sinuata*.

TRIBE COCCINELLINI.

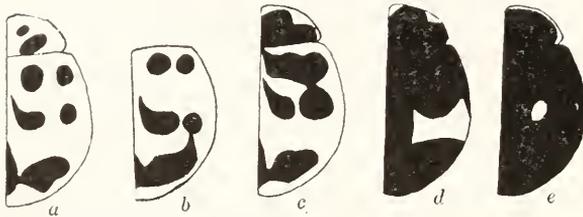
Genus NEOHARMONIA Casey.

3055 a. *Neoharmonia venusta* Mulsant (fig. 44).*Distribution*: Indiana to Kansas, Michigan to Texas.

Var. A Mulsant. The humeral spot united to the lateral spot of the intermediate row.

Var. B. As in fig. 44, b.

Var. C. As in fig. 44, c. The pronotal spots confluent.

FIG. 44.—a to c, variation of color-pattern of *N. venusta*, c, from Louisiana; d, e, *N. notulata*.3055 b. *Neoharmonia notulata* Mulsant (fig. 44).*Distribution*: Louisiana.

Unfortunately I am unable to throw light on the interesting question of the nature of this melanic derivative of the previous species. It is here given specific rank with the greatest hesitancy.

Typical pattern as in fig. 44, d.

Var. C Mulsant. With the light mark reduced and divided into two smaller ones. The lateral one may not reach the margin.

Var. D. As in fig. 44, e.

3055 c. *Neoharmonia ampla* Mulsant.*Distribution*: Texas and Mexico.

The pronotal marks fused to make 2 longitudinal vittæ (fig. 45).

The elytral pattern (fig. 46) is much reduced, revealing in some specimens 4 separate spots instead of 2 in the intermediate row and 4 separate

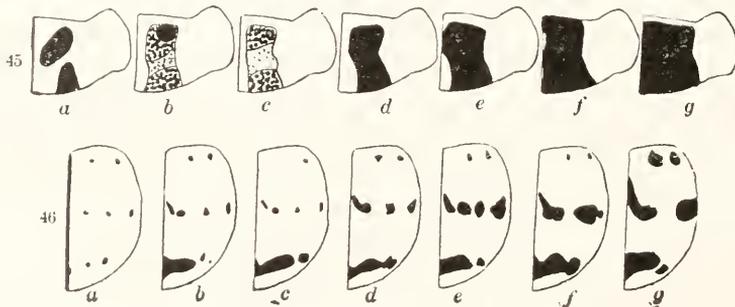


FIG. 45.—Variation in pronotal pattern of *N. ampla*. All from Brownsville, Texas.
 FIG. 46.—Variation in elytral pattern in *N. ampla*. All from Brownsville, Texas.

spots instead of 2 in the apical row. This species stands intermediate in elytral pattern between *Neoharmonia venusta* and *Olla abdominalis* and its variation is parallel in general with the latter.

Genus COCCINELLA Linnæus.

The species of this genus recognized in the United States are shown in fig. 47. Reference to species outside of the United States is necessarily omitted on account of the large size of the genus. The species within the subgenera are closely allied to each other, while the subgenera are far less so.

3056 a. *Coccinella perplexa* Mulsant.

Distribution: North Europe, Siberia, and North America.

Our American species correspond closely to the *Coccinella trifasciata* of Europe and Siberia. It differs in having the black area of the pronotum sharply reentrant, in most cases, at either side of the mesal portion (fig. 48). It is given specific rank with some hesitancy. A comparison of a large series of each would be desirable.

Var. *eugenii* Mulsant. Cephalic band broken (fig. 49).

Var. = *Coccinella trifasciata* var. *fennica* Weise. Intermediate band broken.

Form A. Intermediate band only missing (fig. 49, d).

Form B. Caudal band only missing (fig. 49, j).

Form C. Cephalic band broken and intermediate band only missing (fig. 49, d).

Form D. Cephalic band broken and caudal band only missing (fig. 49, n).

Var. *juliana* Mulsant. Intermediate and caudal bands missing (fig. 49, f). A specimen from Cypress Hills, Long Island, was probably transported there upon plants.

Form E. Intermediate and caudal bands missing, cephalic broken (fig. 49, g.)

Form F. Intermediate band only present. Oregon (fig. 49, o).

Var. *subversa* Leconte. Elytra without pigment. Pacific States (fig. 49, h).

Form G. Black area of pronotum extends to the cephalic edge broadly as in *Coccinella monticola*. Rare. One from Berkeley, California (fig. 49 d).

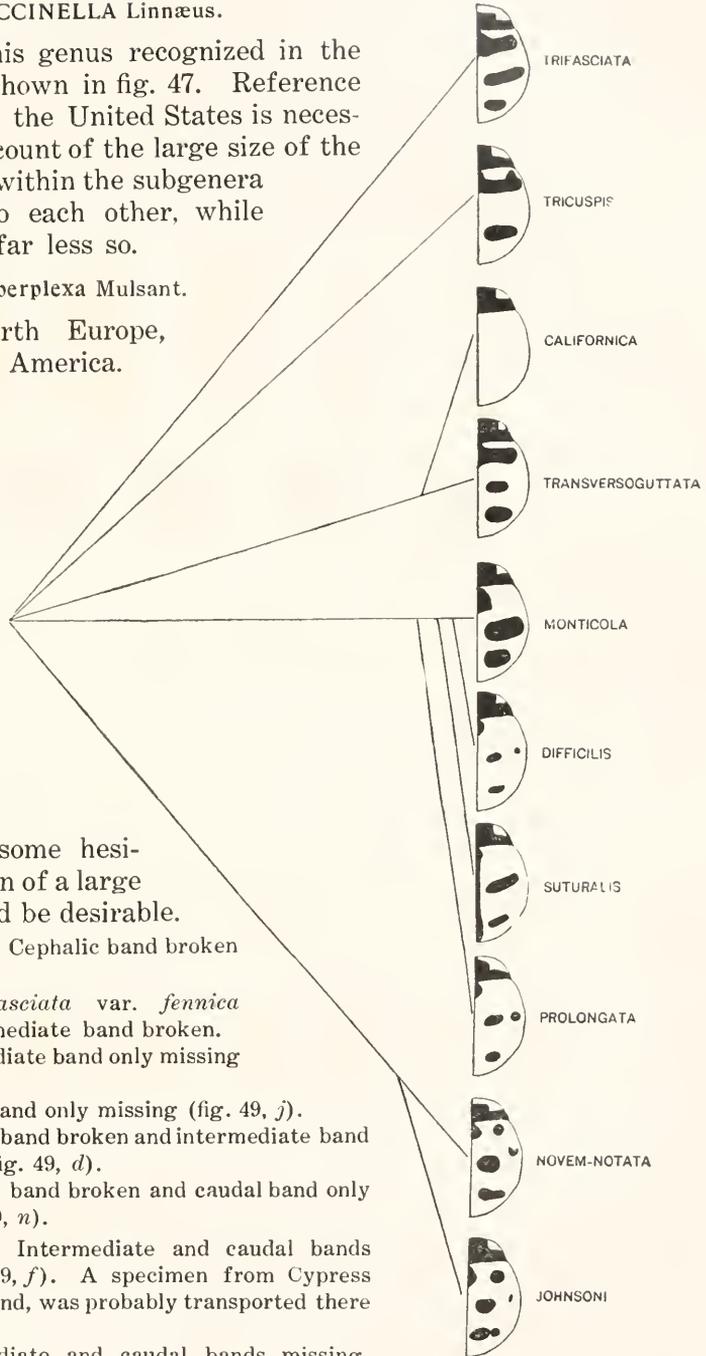


FIG. 47.—The species of *Coccinella* in the United States.

A series collected at random in the botanic garden of the University of California, Berkeley, gave—

Var. <i>subversa</i>	1
Var. <i>eugenii</i>	7
Var. <i>eugenii</i> transition to var. <i>juliana</i>	8
Var. <i>juliana</i>	78
Var. <i>juliana</i> transition to Form <i>C</i>	6
Form <i>B</i>	5
Form <i>A</i>	1
Var. <i>juliana</i> transition to var. <i>perplexa</i>	2
Typical.....	2

Large numbers show that the variety *eugenii* is not as markedly set off from the variety *juliana* as has been stated. This is indicated by the intergrades noted above.



FIG. 48.—Variation in pronotal pattern in *C. perplexa*.
b=mode.

The relationship to *C. novemnotata* suggested by Mulsant is not close, for the larvæ offer a sharp contrast in color. The very closely allied European species *C. trifasciata* shows only one recorded variety (variety *fennica*) in which the intermediate band is broken. This variety was seen only once in one of the heredity experiments referred to later. In eastern North America *C. perplexa* is remarkably constant, but in the West it becomes more and more variable, always, however, in the direction of reduction of pigment.

Subspecies of Oregon characterized by the presence of variety *subversa* and *F*.

Subspecies of California characterized by the presence of *juliana*.

Subspecies of Eastern States: The three bands seldom suffer reduction.

Two mated females kindly sent me by Professor Terhune, from London, Ontario, gave me two fraternities. In one of these all 11 individuals were normal like the parent. In the other fraternity 1 of the 3 individuals corresponded to the variety *fennica* of *C. trifasciata* which I have not seen in *C. perplexa*.

3062. *Coccinella tricuspis* Kirby.

Distribution: Canada and neighboring States.

The elytral pattern of this species is so unique that its relationship is puzzling (fig. 47). The few specimens known show no significant variation.

3058. *Coccinella novemnotata* Herbst.

Distribution: North America.

Var. spots $H+L$, *conjuncta* Fitch. 4 per cent at Cold Spring Harbor (see fig. 52).

Var. spots $H+I$.

Var. spots $I+A$.

Var. spots $\frac{1}{2}+I$. Seen on one side only of 1 specimen from Oyster Bay, Long Island.

Var. spots $L+H+I$.

Var. spots $L+H+I+A$, *confluente* Fitch.

Var. *divisicollis* Fitch. Black pattern of pronotum touching the cephalic margin caudad to the eyes, but not mesad. Known only from Fitch's description. The pronotum is in general relatively constant (fig. 50).

Var. *degener* Casey. The pigment reduced, the apical spot being resolved into two (fig. 51). Probably the specimens of *C. menetriesi* Mulsant, attributed to California, are of this variety. But as Crotch believes that *C. menetriesi* is a variety of *C. undecimpunctata*, the relation of that species to *C. novemnotata* requires further study.

Form A. Some spots lacking.

Var. *franciscana* Mulsant. Elytra without spots.

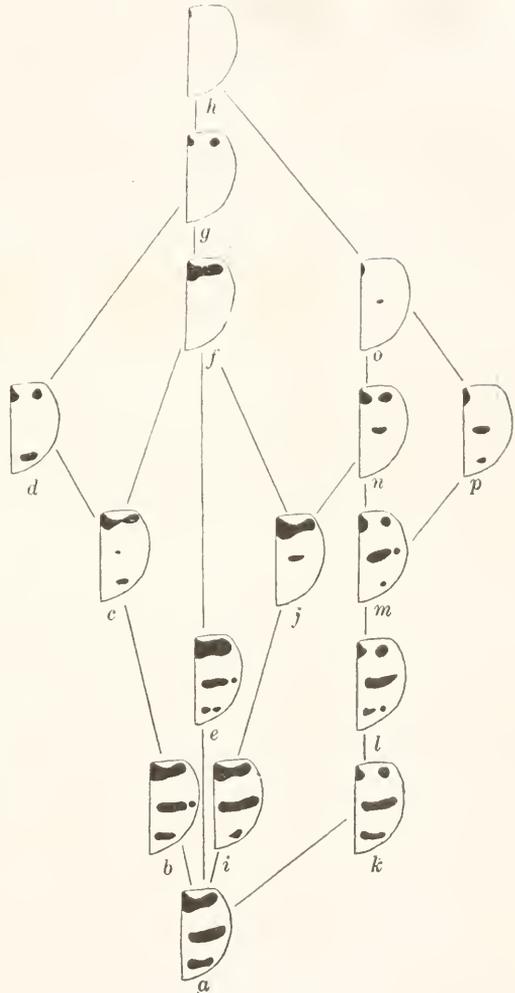


FIG. 49.—Variation of elytral pattern in *C. perplexa*.

Subspecies of the Plateau States: Variety *degener* prevails.

Subspecies of the Pacific Coast: Varieties *degener* and *franciscana* prevail.

MODIFICATION AND HEREDITY.

The application of 40° C. to the prepupæ and pupæ did not affect the pattern. The results of the experiments in heredity with this species are summarized in table 17. Since on Long Island the variety *conjuncta* was



FIG. 50.—Variation in pronotal pattern in *Coccinella novemnotata*. *b*=mode.

present in a ratio of 4 per cent, and each of the other varieties was found in less than 0.1 per cent, the mates of females from nature were probably normal. The progeny of such a female (278) are represented in fig. 52. They are remarkable, since 40 per cent of the progeny surpass the unusually pigmented mother in the amount of confluence of spots. It is hard to believe that this is not determinate. The lack of intergrades between the 4 normal specimens and those like the mother is striking, especially in comparison with the experiment of 440 ♀, and with the presence of such intergrades in nature. In general, the conclusion is

TABLE 17.—Heredity in *Coccinella novemnotata*.

Father.		Mother.		No.	Nor.	<i>h+l</i>	<i>h tr. l</i>	<i>h tr. l,</i> <i>h tr. m</i>	<i>h+l,</i> <i>h tr. m</i>	<i>h+l+m</i>
No.	Elytral pattern.	No.	Elytral pattern.							
—	—	278 ♀	<i>h+l+m</i>	20	4	0	0	0	0	8
440 ♂	<i>h+l</i>	440 ♀	<i>h+l+m</i>	55	23	3	0	0	19	4
+—	<i>h tr. m</i>									
405 ♀	<i>h+l</i>	405 ♀	nor.	46	39	5	0	0	0	0
+—	<i>h tr. m</i>									
*449 ♂	<i>m+a</i>	*449 ♀	<i>m tr. a</i>	14	6	0	0	0	0	0
—	—	465 ♀	<i>h ap. l</i> <i>h ap. m</i>	24	16	2	5	1	0	0
Total.....				159	88	10	5	1	19	12

Father.		Mother.		No.	<i>h+l+m</i> <i>m tr. a</i>	<i>h+l</i> <i>m+a</i>	<i>h+l+</i> <i>m+a</i>	<i>h+l</i> <i>h tr. m</i> <i>m+a</i>	<i>m tr. a</i>	<i>m+a</i>
No.	Elytral pattern.	No.	Elytral pattern.							
—	—	278 ♀	<i>h+l+m</i>	20	5	0	3	0	0	0
440 ♂	<i>h+l</i>	440 ♀	<i>h+l+m</i>	55	3	0	1	1	1	0
+—	<i>h tr. m</i>									
405 ♀	<i>h+l</i>	405 ♀	nor.	46	0	0	0	0	0	2
+—	<i>h tr. m</i>									
*449 ♂	<i>m+a</i>	*449 ♀	<i>m tr. a</i>	14	0	1	0	0	2	5
—	—	465 ♀	<i>h ap. l</i> <i>h ap. m</i>	21	0	0	0	0	0	0
Total.....				159	8	1	4	1	3	7

*Progeny of 405.

justified that there are here a number of positions of organic stability, namely, *h+l*, *h+l+m*, *m+a*, *h+l+m+a*; *h+m* was never seen without other confluence either in these experiments or wild. In progeny from 465 ♀ (fig. 53) we see that an unusual shape of the humeral spot is inheritable. The amount and kind of intergradation varies in fraternities from different parents, and from this we may infer that we are not dealing with sharp-cut unit-characters, but rather with positions of organic stability not finely localized.

3058 a. *Coccinella johnsoni* Casey.

Distribution: San Diego, California.

This species (fig. 47) is obviously a derivative of *C. novemnotata*. Since *C. novemnotata* has the pronotal black free from the cephalic margin throughout its range and throughout all of its variations from the lightest variety, *franciscana*, to the darkest variety, *confluente* (excepting the very rare and peculiar variety *divisicollis*), it is probably entitled to specific rank. No typical specimen of the Western subspecies of *C. novemnotata* has been collected in Southern California to my knowledge. A large series is necessary to fix its status more definitely.

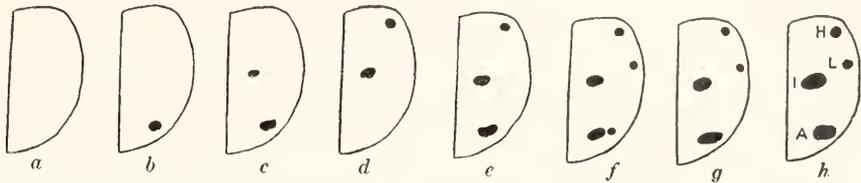


FIG. 51.—Variation of elytral pattern of *C. novemnotata* in the Western States. *f*—mode.

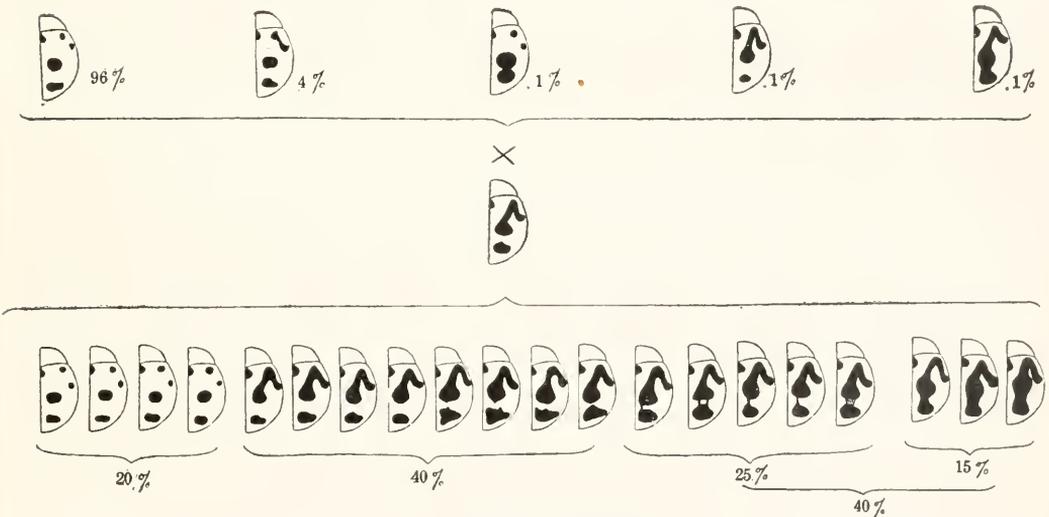


FIG. 52.—Pedigree from 278.

3059. *Coccinella transversoguttata* Faldermann.

Distribution: Europe, Siberia, and North America.

Typical pattern: With a lateral spot. (See fig. 54, *g*.)

Var. *quinenotata* Kirby. The lateral spot absent (fig. 54, *d*, *e*).

Var. *nugatoria* Mulsant. The basal band broken. Common in the Western States and Mexico (fig. 54, *c*).

Form A. Lacking humeral spot (fig. 54, *a*). Very rare. Seen only in Eastern Washington. It is an extreme fluctuation of the reduction of pigment of the basal band characteristic of that region.

The typical pattern is rare with us. Nearly all of our specimens in North America are of the variety *quinquenotata*. The variety *nugatoria* is common in the Western States, but not in the Eastern. Mulsant states that it is found more often in the south of Europe than in the north. Further knowledge of this distribution would be desirable. The extreme of pigment reduction shown is the form *A* from Washington. This is in good accord with the general belief that *C. californica* is a spotless derivative of *C. transversoguttata* and favors the idea of their close relationship. The variation in the pronotum is shown in fig. 55.

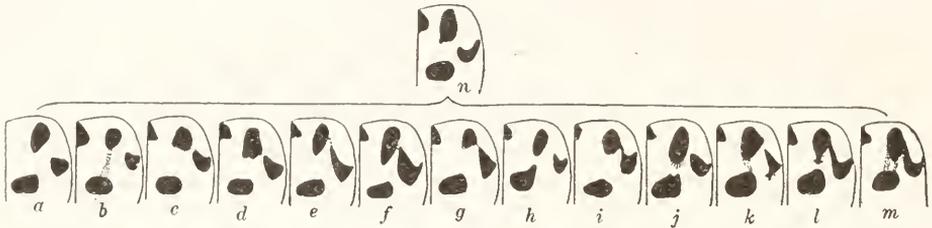


FIG. 53.—Offspring of 465.

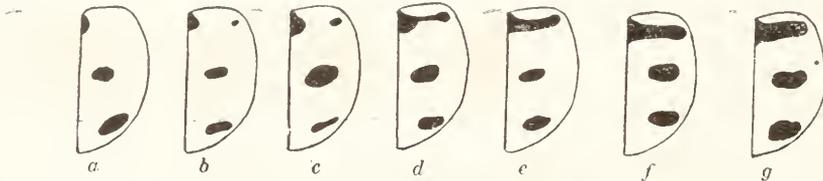


FIG. 54.—Variation of elytral pattern of *C. transversoguttata*, *a*, from Spokane, Washington; *b* to *e*, from Kamloops, British Columbia; *f*, from Stony Lake, Michigan; *g*, from Wollaston, Massachusetts.

3059 a. *Coccinella californica* Mannerheim.

Distribution: Pacific States.

The small, yellowish basal area near the scutellar spot is present in greater or less degree, the variation being continuous. The suture is pigmented ordinarily in California (see fig. 56), but in some cases approaches variety *nevadica*.

Var. *nevadica* Casey.

The suture not pigmented back of the scutellar mark. Reno, Nevada.

Var. *melanocollis* n. var.

Pronotum entirely black (fig. 57); 2 specimens from Berkeley.

Two round white spots on the head found in this species and *C. transversoguttata* make it not unlikely that it is a derivative of that species. Unfortunately I was not able to make this cross. *C. californica* males were mated with both *C. monticola* and *novemnotata* and found to be intersterile.

3060. *Coccinella monticola* Mulsant.

Distribution: New England to the Pacific.

In degree of confluence of the elytral spots *Coccinella monticola* (fig. 58) gives the following varieties which have pronota as shown in fig. 59:

Var. *sellica* n. var. $\frac{1}{2}$ + median band. California and New Hampshire. (Fig. 58, d.)

Var. *postica* n. var. Median band + apical band. California. (Fig. 58, e.)

Var. *confluenta* n. var. $\frac{1}{2}$ + median band + apical band. California. (Fig. 58, e.)



FIG. 55.—Variation of pronotal pattern in *C. transversoguttata*. Mode *a* to *b*.

The following patterns (fig. 60), although they appear at first glance very different from variety *monticola*, are nevertheless placed here, with some reservation, because of the intergradation from *C. monticola* in the direction of reduction of pigment in some localities. In any one locality the amount of pigment is tolerably constant. It seems to me probable that this amount in *C. monticola* is a result of environmental influence. The variation in their pronota is given in fig. 61.

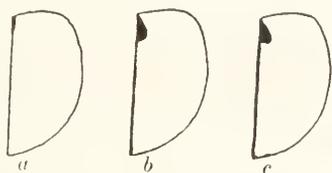


FIG. 56.—Variation of elytral pattern of *C. californica*. *b*—mode.



FIG. 57.—Variation in pronotal pattern in *C. californica*. *b*—mode; *d*, variety *melanocollis*.

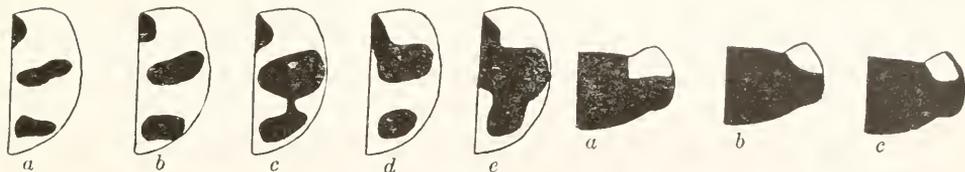


FIG. 58.—Variation in elytral pattern in *C. monticola*. *b*—mode.

FIG. 59.—Variation of pronotal pattern in *C. monticola*. *b*—mode.

Var. *alutacca* Casey. Pigment of median band so reduced as to result in complete or partial isolation of a lateral spot. Colorado and westward. (Fig. 60, e, d.)

Aberration *impressa* Casey. Similar, with "an impression along the side margin of the pronotum extending arcuately inward just before the middle, disappearing from the edge." This unique specimen is probably an aberration. The type specimen may never be duplicated, or at least may not become established. California.

Var. *sonorica* Casey. The median band much reduced with the lateral spot absent. Colonia Garcia, Chihuahua, Mexico. (Fig. 60, b.)

Var. *biguttata*. Pigment much reduced. Lateral and apical spots absent. Buena Vista, Colorado. (Fig. 60, a.)

3061 a. *Coccinella difficilis* Crotch.

Distribution: Utah.

Although the pattern of this species (fig. 47) is very close to that of *C. monticola* var. *alutacea*, it is probably entitled to specific rank. This is because of its small size and the fact that the two elements of the median row of elytral spots vary in the direction of greater pigmentation by increase in general dimensions rather than by confluence. Specimens are as yet too few to make its status and relationship clear.

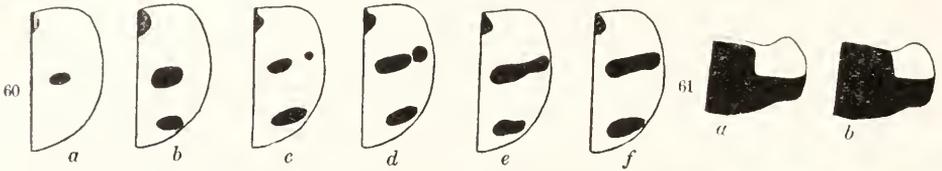


FIG. 60.—Variation of elytral pattern in *C. monticola* var. *alutacea* and *biguttata*.
FIG. 61.—Pronotal pattern of *C. monticola* var. *alutacea*. a, a single specimen.

3061 b. *Coccinella suturalis* Casey.

Distribution: Colorado.

This is very clearly a derivative from *C. monticola* var. *alutacea* by the addition of the pigmented suture—a repertoire variation. Its specific rank rests largely upon the reduced height of the elytra.

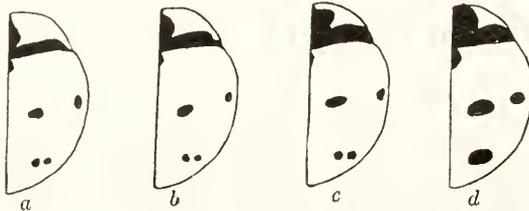


FIG. 62.—Variation in color-pattern in *C. prolongata*.
a, b, c, from Cheney, Wash.; d, from Utah.

3061. *Coccinella prolongata* Crotch.

Distribution: Kansas to Pacific Coast.

The elytral pattern is essentially that of *C. monticola* var. *alutacea*, from which it is probably derived, but with the pigment still further reduced. The pronotal pattern is striking, and although there is some intergradation, it is apparently interrupted (fig. 62). The essential characteristic is not only the prolongation of the white area of the pronotum, but the spindle shape of the central portion of the back area cephalad as well as caudad. Its nearest allies have the black pattern extending along the cephalic edge for half its width.

Genus CYCLONEDA Crotch.

The color-pattern and its lines of variation in this genus are markedly different from *Coccinella*, of which Leng makes it a subgenus. The form, agility, and the difference of the food of the larvæ (Johnson, 1907) support the generic distinction. The sexual difference alleged to exist in the pronotal pattern, though noticeable, is much less than indicated by Mulsant and Dimmock.

3064. *Cycloneda sanguinea* Linnæus.

Distribution: Cuba, Bahamas, Florida to California.

Var. *immaculata* Fabricius. With pale spots on pronotum inclosed. Florida to Louisiana.

The sexual differences in the median emargination of the black pronotal area is either absent or slight.

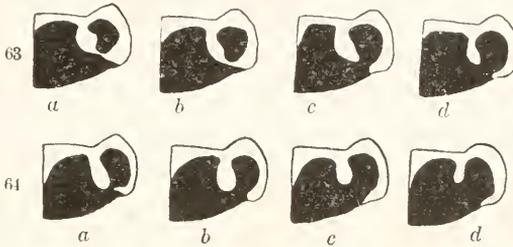


FIG. 63.—Variation in pronotal pattern of *Cycloneda munda* male. *a*, *b*, from Cold Spring Harbor, New York; *c*, *d*, from Stony Lake, Michigan.

FIG. 64.—Variation in pronotal pattern in *Cycloneda munda* female.

3064 a. *Cycloneda munda* Say.

Distribution: Northeastern and North Central States.

The males have a greater amount of pigment laterally on the pronotum, but the median emargination of the black pattern is much deeper (figs. 63 and 64). This species, closely allied to the preceding, is recognized because of Dimmock's statement that the larvæ differ specifically.

Var. *polita* Casey.

Having the scarlet color of *C. sanguinea* (figs. 65 and 66). It will probably prove to be a variety, because in its range, the northwestern States, yellowish individuals are occasionally met with. It is possible, however, that these specimens are caused by different degrees of fading.



FIG. 65.—Variation of pronotal pattern in *C. munda* var. *polita* male.

FIG. 66.—Variation in pronotal pattern of *C. munda* var. *polita* female.

3064 b. *Cycloneda ater* Casey.

Locality unknown.

This wholly black species is paralleled only by *A. lugubris*.

Genus OLLA Casey.

The color-pattern in this genus is so diverse in its elements and lines of variation from *Coccinella* that I believe that it is entitled to more than the subgeneric rank which Leng gives it. It has stronger resemblances to *Neoharmonia ampla* in its color-pattern than to any *Coccinella*.

3065 a. *Olla abdominalis* Say.

Distribution: Indiana to Texas, Arizona to California.

The crescentic shape of the subsutural intermediate spot has its parallel in *Neoharmonia venusta* and *ampla* and one specimen of *H. convergens*. The variation in the color-pattern of the pronotum is given in fig. 67.



FIG. 67.—Variation of pronotal pattern of *O. abdominalis*. *b*=mode.

Var. *semilunaris*, n. var.

The subsutural and intermediate spots of the intermediate row are fused and extended towards the apex to make a bowl-shaped mark (fig. 68). This extension is a unique feature, for it is not an equilateral enlargement nor a confluence of spots, but a determinate extension in one direction. Arizona and Texas.

Var. *minuta* Casey.

The elements of the intermediate row and the apical spot are confluent, but with reentrant angles (fig. 68). Brownsville, Texas.

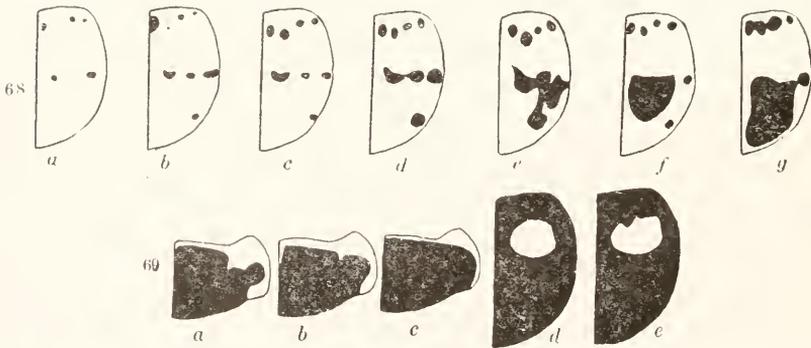


FIG. 68.—Variation in elytral pattern in *O. abdominalis*. *f*, var. *minuta*; *g*, *h*, var. *semilunaris*.
FIG. 69.—Variation of color-pattern in *O. plagiata*. All from Arizona.

3065 b. *Olla plagiata* Casey.

This is the melanic derivative of *Olla abdominalis* (fig. 69) and may be found to be intergenerating. In the meanwhile it is best considered distinct. The Florida specimens differ, Casey says, as well as those from Las Vegas, Mexico, but the difference is slight and, in the lack of a large series, they will not be described here.

Genus ADALIA Mulsant.

3068. *Adalia bipunctata* Linnæus.

Distribution: Europe and Eastern and Central States.

Typical pattern: Spots 2+3. Double nature of the band not apparent.

Form *pruni* Weise.

Spots 2+3. Double nature of spot apparent. About 1 per cent at Cold Spring Harbor.

Var. *herbsti* Weise.

Spots 2, 3. I have not yet seen this variety in America, but it may be confidently expected because of the occurrence of form *pruni* and the probability that when found it has been considered to be the *A. frigida* var. *parvula*.

Var. *rubiginosa* Weise.

Spots 1, 2+3. Less than 1 per cent at Cold Spring Harbor.

The 17 other varieties given by Weise (1879), nearly all of which show greater amounts of pigment, have not yet been recorded from America with the exception of—

Var. *quadrifasciata* Scopoli = *humeralis* Say?

Elytra black, except for a reddish humeral area and a reddish spot near the suture at $\frac{2}{3}$. Widely distributed, but always uncommon.



FIG. 70.—Variation in pronotal pattern in *A. bipunctata*. *c*—mode.

Subspecies of North America: The lack of all varieties with the exception of *pruni*, *rubiginosa*, and *quadrifasciata*, is typical of North America as a whole. While some of the other varieties will be found, they will be great rarities, and one may say that North America is characterized by the general lack of the dark varieties, excepting the *quadrifasciata*.

Burgess (1903) has found the variety *quadrifasciata* and the typical species to be intergenerating. The heredity was perfectly segregate. The variety *quadrifasciata* is found in Europe in company with numerous varieties which intergrade toward the typical species and to the almost or wholly melanic variety *lugubris*. It is singular that with us these other varieties should be absent, leaving only the variety *quadrifasciata*. It can not be because variety *quadrifasciata* is a position of much greater organic stability, because in Germany (Schroeder, 1901) it is greatly outnumbered by the allied variety *sevpustulata*, which is less melanic. It justifies the view that at least some of these varieties are not merely ontogenetic in origin or fluctuations, but true varieties representing inheritable positions of organic stability.

The pronotum in the dark variety *quadrifasciata* is black, with only a very light lateral margin which may not be complete. The type and light varieties have a range of variation shown in fig. 70. This exceeds that shown in Europe in the direction of less pigment. The longitudinal median mark fails in only 3 cases in 97. I have not seen any of our specimens with a totally black pronotum, such as is known in Germany.

From 1 impregnated female of variety *rubiginosa* I raised 3 beetles; 2 were of the typical species and 1 of the variety *rubiginosa*, with the spot slightly smaller than the parent. The heredity is therefore segregate.

3066. *Adalia frigida* Schneider.

Distribution: Lapland, Siberia, and United States.

Typical pattern: Spots 1, 2+3, 4+5. Rare. Found by Casey in Colorado and named by him *ornatella* (fig. 71).

Var. *immaculata* n. var. No spots. Unknown from Europe.

Var. *melanopleura* Leconte. Spot 1. Colorado. Unknown from Europe.

Var. *parvula* Weise. Spots 2, 3. Our commonest variety in North America.

Var. *siberica* Weise. Spots 2+3. One from Tyngsboro, Massachusetts.

Var. *fasciata* Weise. Spots 1, 2+3, 4+5. One from Springfield, Massachusetts.

Var. *postica* n. var. Spots 1, 2, 3, 4+5. Two from Springfield, Massachusetts.

Var. *hyperborea* Paykull. Spots 1+2+3, 4+5.

Var. *humeralis* Say or n. var. Has the pattern of *A. bipunctata* var. *quadrifasciata*. Widely distributed, nowhere common. It is uncertain whether the *A. humeralis* Say was an *A. bipunctata* or *A. frigida*. Since the name *quadrifasciata* Scopoli antedates it for the variety of *A. bipunctata*, I apply *humeralis* to the corresponding variety of this species.

Weise names 13 other forms showing various other combinations of absence or confluence of some of the 5 spots. Most, if not all of these, will probably be found in the United States eventually. The forms with absence of 4 and 5 constitute a variety as well as those without any spot. The other patterns are forms of the typical species or of these varieties.

The pronotum shows variation (fig. 72) from an M pattern with 2 lateral spots, in which it approaches that of *A. bipunctata*, to one with pigment so reduced as to reveal a number of elements nearly identical with those of *Cleis picta* and *Olla abdominalis*, closely allied genera. The following forms of pronotal pattern may be recognized. None of these are of varietal rank and the amount of pigment has only a low correlation with the amount on the elytra.

Form A. The M-pattern so reduced that the component elements are readily recognized. The lateral spots separate.

Form B. The M-pattern apparent, and resembling that of *A. bipunctata*. The lateral spots separate.

Form C. The M-pattern heavier, with lateral spots narrowly united.

Form D. The M-pattern much extended, with lateral spots broadly united, the pigment encroaching so as to leave 2 light spots at caudal margin instead of 1.

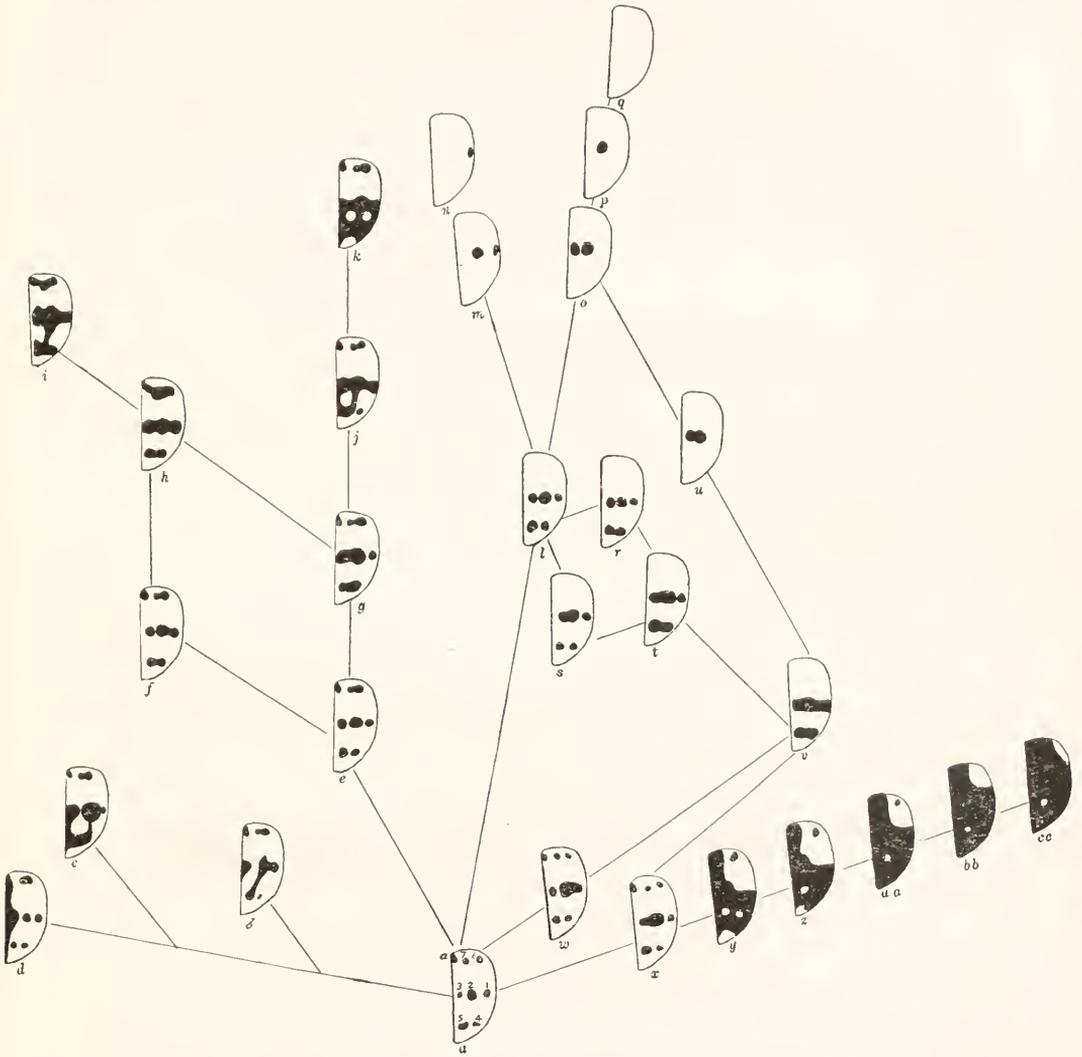


FIG. 71.—Elytral variation of *Adalia frigida* and *connectans*.

Subspecies of North America: The typical condition in Europe is not common with us. The variety *parvula* far exceeds it in numbers.

The case of the variety *humeralis* is especially interesting. In the Eastern States where *A. bipunctata* is found, many specimens with this pattern belong to *A. bipunctata*, as is known by the cross-breeding obtained by Burgess. The *humeralis* pattern is found, however, throughout the Rocky Mountains and Pacific States, where *A. frigida* and *annectans* occur but not *A. bipunctata*. In fact, this pattern is more abundant there than in the East. Since the two species are closely allied and each is known to give many variations in the melanic direction which show many analogies, I believe that this pattern exists as a variety of each. It becomes necessary to consider these western specimens as variety *humeralis* of *A. frigida* or variety *humeralis* of *A. annectans*.

TABLE 18.—Heredity in *Adalia frigida*.

Mother, variety.	No.	Offspring.					
		Parvula.	Sibirica.	Postica.	Faceta.	Hyperborea.	Immaculata.
Spots present.....	..	2, 3	2 + 3	1, 2, 3, 4 + 5	1, 2 + 3, 4 + 5	1 + 2 + 3, 4 + 5	No spots.
265 ♀.....	4	M 3	1
269 ♀.....	7	M 2	1	1	2	1
285 ♀.....	1	M	1

Three specimens that were kindly sent to me by Mr. G. W. Dimmock, of Springfield, Massachusetts, that proved to be impregnated females with spots 2 and 3 only, gave offspring as in table 18. It will be noticed that where spots 4 or 5 are present at all they are well developed, thus constituting a unit-character.



FIG. 72.—Variation in pronotal pattern in *Adalia frigida*.

3063. *Adalia annectans* Crotch.

Distribution: Western States and British Columbia.

Lack of intergrades and of breeding experiments make it desirable to retain the specific status of this pattern for the present, in spite of its close relation to *A. frigida*. (See fig. 71.)

Typical pattern: Spots *a*, 1, 2, 3, 4, 5, 6, 7. The numbering is that of Weise, with 6 the humeral spot, and 7 next it.

- Form A. Spots 1 + 2, 3, 4, 5, 6, 7, $\frac{1}{2}$.
 Form *ovipennis* Casey. Spots 1, 2, 3, 4, 5, 6 + 7, $\frac{1}{2}$.
 Form B. Spots 1 + 2, 3, 4, 5, 6, 7, $\frac{1}{2}$.
 Form C. Spots 1 + 3, 2, 4, 5, 6, 7, $\frac{1}{2}$.
 Form D. Spots 1 + 2, 3, 4, 5, 6 + 7, $\frac{1}{2}$.
 Form E. a, 1 + 2, 3, 4 + 5, 6 + 7, $\frac{1}{2}$.
 Form F. a, 1 + 3, 2, 4 + 5, 6 + 7, $\frac{1}{2}$.
 Form G. 1, 2, 3, 4, 5, 6 + 7 + $\frac{1}{2}$.
 Form H. 1 + 2 + 5, 3, 4, 6 + 7 + $\frac{1}{2}$.
 Var. *transversalis* Casey. Spots 1 + 2 + 3, 4 + 5, 6 + 7, a.
 Form I. Spots (1 + 2 + 3) + (4 + 5), 6 + 7 + a.
 Form J. Spots 1 + 2 + 3 + 5 + suture, 4, 6 + 7, a.
 Form K. Spots (1 + 2 + 3) + (4 + 5) + suture + margin, 6 + 7.

Var *sexpustulata* n. var. \subset *A. bipunctata* var. *sexpustulata*.

The black humeral spot within the reddish humeral area places it as variety of this species rather than as *A. frigida*. Hood River, Oregon.

Var. *ocellata* n. var.

Specimens with the black pigment revealing 2 light spots on the dark ground instead of 1 as above. Hood River, Oregon.

Var. *humeralis* n. var. \subset *A. bipunctata* var. *quadrimaculata*.

The black humeral spot within the humeral reddish area place it as a variety of this species rather than *A. frigida*. Widely distributed.

Most of the species of the dark varieties given above are in the Schwarz collection of the U. S. National Museum, and were collected at Hood River, Oregon. They seem rare elsewhere, but this may be because they were more diligently sought there.

The pronotum of this species shows variation closely parallel to that of *A. frigida*. So far I have seen only the patterns given in fig. 72. The other patterns of *A. frigida* may, I believe, be looked for in this species when larger series become available.

The legs of this species (at least of its light varieties) in Spokane County, Washington, are uniformly yellowish-brown and there is an area of the same color on the ventral surface of each segment of the abdomen, which in *A. frigida* is nearly black. Larvæ brought from Washington to Cold Spring Harbor emerged here with the western color. None were raised in the East, however, from the egg.

Genus *CLEIS* Mulsant.3069. *Cleis picta* Rand.

Distribution: Northern United States and Canada.

This species is certainly not congeneric with many of those placed in *Harmonia* by Mulsant, as shown by the pronotal pattern, which shows much more affinity to *Adalia*. The pronotal and elytral variation as shown in figs. 73 and 74 is great and apparently continuous.

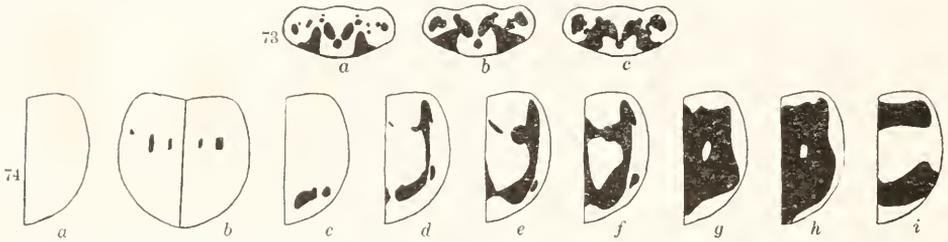


FIG. 73.—Variation of pronotal pattern of *Harmonia picta*. *b*=mode.

FIG. 74.—Variation in elytral pattern of *Harmonia picta*. *e*=mode; *b, c*, from Tyngsboro, Massachusetts; *d, e, f*, from Wisconsin; *g, h*, from New Jersey; *i*, from New Mexico.

Var. *blanchardi*, n. var.

Elytra without black pigment. Throughout the range. Named in honor of Mr. F. Blanchard, who has kindly called my attention to the fact that this is not a sex difference. The former view that this spotless pattern was that of the male arose from the fact that it is much more numerous among the males.

Form *A*.

Pattern reduced to a few small marks, as in fig. 74, *a* and *b*. Two specimens from Tyngsboro, Massachusetts. It is improbable that this form is limited to Massachusetts. Similar vigilance should reveal it elsewhere.

Form *minor* Casey. The costal spot at $\frac{3}{4}$ confluent with the vitta and margin (fig 75).

Form *contexta* Mulsant. Basal band continues from vitta to suture.

Form *concinata* Mulsant. The elytra nearly black.

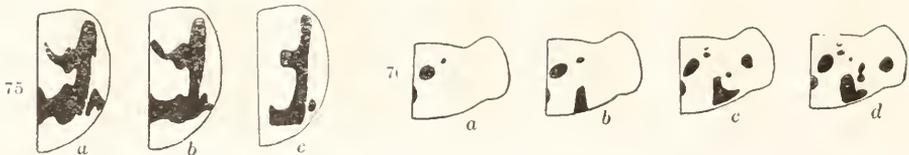


FIG. 75.—Elytral pattern of 3 Western specimens of *Harmonia picta*. *a*, from Paradise Park; *b*, from Washington; *c* from Vela Pass, Washington.

FIG. 76.—Variation in pronotal pattern in *Harmonia hudsonica*. *a*, from Carrs Peak; *b*, from Palmetz, Arizona; *c*, from Whitefish Point, Lake Superior; *d*, from Marquette, Michigan.

Subspecies of Pacific Coast characterized by form *minor* and intergrades to it.

Subspecies of New Jersey characterized by the presence of the very dark patterns.

3069 a. *Cleis hudsonica* Casey.

Distribution: Boreal Zone in Canada, Wisconsin, Michigan, Mount Washington, New Hampshire, and Black Mountain, North Carolina.

The variation, while considerable, as shown in figs. 76 and 77, is apparently continuous. It does not intergrade with *C. picta*, for the pattern is made up of different elements.

Genus AGRABIA Casey.

3070. *Agrabia cyanoptera* Mulsant.

Distribution: Mexico, New Mexico and Arizona.

While the peculiar blue color is something quite different from its allies, the pronotal pattern (fig. 78) points to a relationship with *Neoharmonia*. It is probable that its blue color is a feature of relatively recent acquisition.

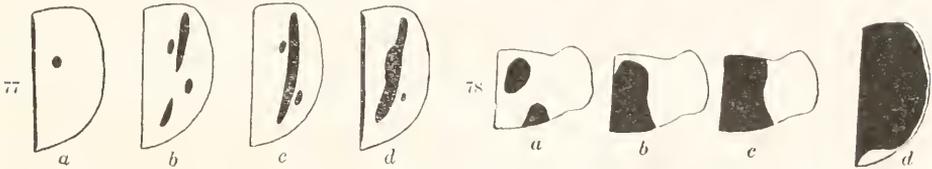


FIG. 77.—Variation of the elytral pattern in *Cleis hudsonica*. *c*—mode; *a*, *d*, from Palmerly, Arizona; *b*, from New Hampshire.
FIG. 78.—Variation in color-pattern in *Agrabia*. All from Huachuca Mountains, Arizona.

Genus ANISOCALVIA Crotch.

3072. *Anisocalvia duodecimmaculata* Gebl. (Fig. 79.)

Distribution: Lake Superior, Hudson Bay, British Columbia, and Siberia.

Form *elliptica* Casey. The two spots, transversely placed at middle of the elytra, confluent.

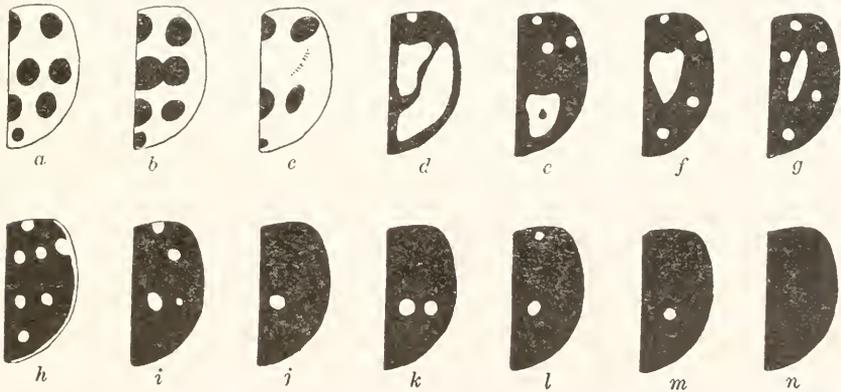


FIG. 79.—Variation of elytral pattern. *Anisocalvia duodecimmaculata*: *a*—mode; *a*, from Oregon; *b*, from Hudson Bay. *Anisocalvia quatuordecimguttata*: *h*—mode; *c*, *d*, from Montana; *e*, from Marquette, Michigan; *f*, from Catskill Mountains; *g*, from Canada; *h*, *j*, *k*, *n*, from British Columbia; *i*, from Hudson Bay; *l*, from Massachusetts; *m*, from Hood River, Oregon.

3071. *Anisocalvia quatuordecimguttata* Linnæus.

Distribution: Northern United States and Canada.

There is in the Museum of Comparative Zoology a very large series of the beetles of this species, or at least of this genus, collected by Mr. H. E. Morse, at Lake Champlain. At the time of my visit to the museum they could not be found. Until this much-needed series can be carefully studied a revision of this genus is inadvisable. All the patterns are therefore given in fig. 79, with no attempt to define their status. Some are said to exist in one sex only, but this requires investigation.

Genus ANATIS Mulsant.

3075. *Anatis quindecimpunctata* Oliv.

Distribution: Northeastern United States and Canada.

The dark form mentioned by Leng may well be an age difference, so much does appearance change in specimens when kept alive. There is, however, variation of spots (figs. 80 and 81).

Form A. Inner apical spot absent.

Form B. Scutellar and subsutural intermediate spots confluent.

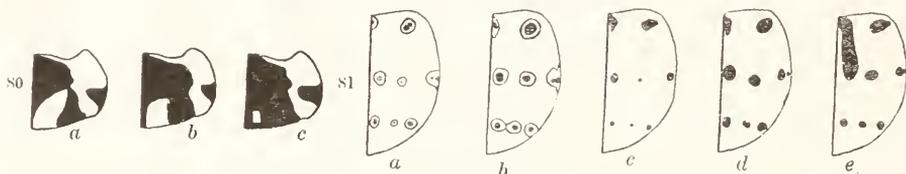


FIG. 80.—Variation in pronotal pattern in *Anatis quindecimpunctata*. *b*—mode. All from Stony Lake, Michigan.

FIG. 81.—Variation of elytral pattern of *Anatis mali* and *quindecimpunctata*. *a* and *b*—*o mali*. All from Stony Lake, Michigan.

3075. *Anatis mali* Say.

Distribution: Michigan, Indiana, Wisconsin, Idaho, and Washington.

The variation of the pattern (figs. 81 and 82) seems to be continuous. There are intergrades of *A. quindecimpunctata* towards the two costal spots of *A. mali*. The pronotum and shading of elytra, however, distinguishes it sharply from *A. quindecimpunctata*. Its range is within that of *quindecimpunctata*, which is probably the parent species.



FIG. 82.—Variation of pronotal pattern in *Anatis mali*. *a*—mode. All from Stony Lake, Michigan.

FIG. 83.—Variation of color-pattern of *Anatis lecontei*. From Southern Arizona.

3076. *Anatis rathvoni* Leconte.

Distribution: California and Oregon.

Form A. With some or all of the spots placed as in *A. quindecimpunctata* indistinctly indicated.

3076 a. *Anatis lecontei* Casey.

Distribution: Colorado, New Mexico, and Arizona.

The black limb is variable in extent (fig. 83).

Form A. Without the basal spots on the pronotum. Throughout the range.

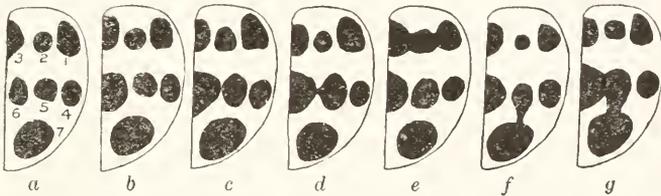
TRIBE EPILACHNINI.

Genus EPILACHNA Chevrolat.

Epilachna borealis Fabricius.*Distribution:* Eastern United States.*Type:* Spots 1, 2, 3 + suture, 4, 5, 6 + suture, 7 (fig. 84, *b*).Form spots 1, 2, 3 + suture, 4, 5 + 6 + suture, 7 (fig. 84, *d*); 6 in 156 = 4 per cent of females and 27 in 214 = 13 per cent of males at Cold Spring Harbor, New York.Form spots 1, 2, 3 + suture, 4, 5, 6, 7; 3 per cent at Cold Spring Harbor (fig. 84, *a*).

Form spots 1, 2 + 3 + suture, 4, 5, 6 + suture, 7; 2 in 370 = 1— per cent at Cold Spring Harbor.

Form spots 1, 2 + 3 + suture, 4, 5 + 6 + suture, 7; 1— per cent at Cold Spring Harbor.

Form spots 1 + 2 + 3 + suture, 4, 5, 6 + suture, 7; 1— per cent at Cold Spring Harbor (fig. 84, *e*).Form spots 1, 2, 3 + suture, 4, 7 + 5 + 6 + suture; 1— per cent at Cold Spring Harbor (fig. 84, *g*).Form spots 1, 2, 3 + suture, 4, 6 + suture, 6 + 7; 1— per cent at Cold Spring Harbor (fig. 84, *f*).FIG. 84.—Variation of the elytral pattern of *E. borealis*. *b*—mode; *a* to *g*, from Cold Spring Harbor, N. Y.FIG. 85.—Variation in the pronotal pattern of *E. borealis*. *c*—mode. *a* to *f*, from Cold Spring Harbor, New York.

Although not a color variation, 1 specimen with an emarginate pronotum cephalad seems worthy of mention here. It did not appear in any way pathological or traumatic. Intergrades are so numerous and the inheritance of these forms is so imperfect that they do not deserve varietal rank. No geographical differences are known in the range, except that it has given way to its derivative, *E. toweri*, in Texas and vicinity. The pronotum shows a wide range of variation in the amount of pigment (fig. 85), which the modification and heredity experiments given later show to be largely the result of modification. There is, however, one distinct variety.

Var. *A*. Lacks lateral pronotal spots; 1— per cent at Cold Spring Harbor (fig. 85, *a*).

HEREDITY.

Since it is difficult to get two broods through in a year and since the loss in hibernation is heavy, the experiments were frequently interrupted at the end of one generation (table 19). The death-rate from hibernation of the forms with confluence of spots was higher. This matter should be

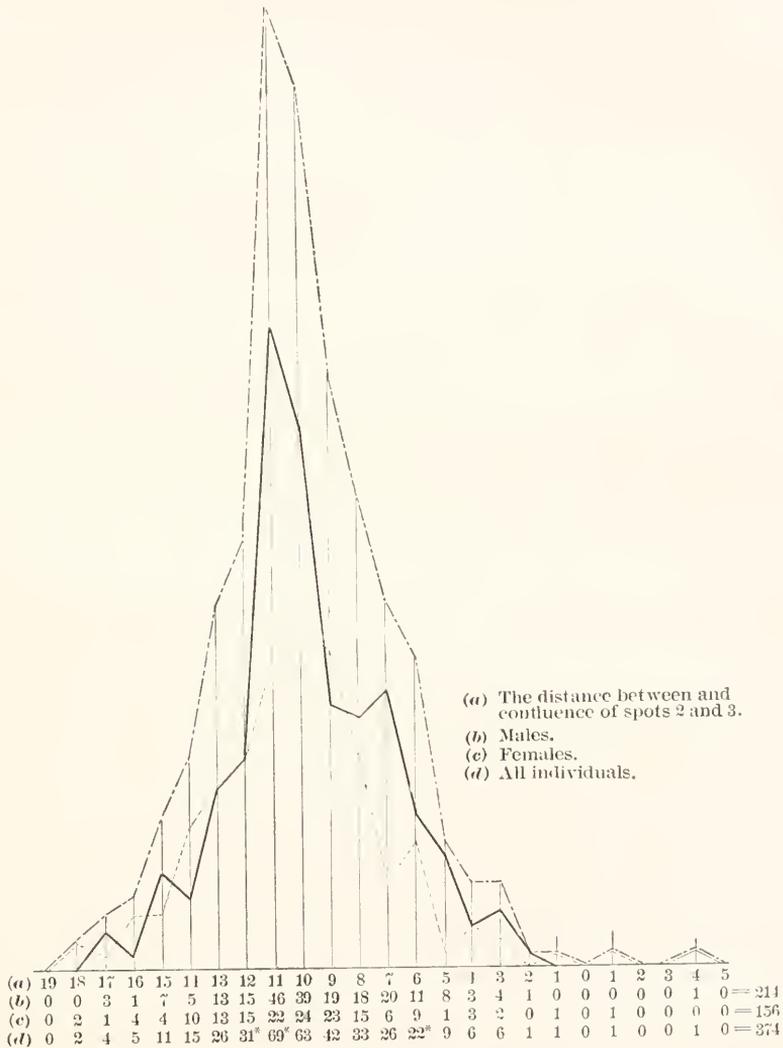


FIG. 87.—Variation of distance between and confluence of spots 2 and 3 in *Epilachna borealis* at Cold Spring Harbor, New York.

experimentally tested with large numbers. The heredity of the forms with confluence differs from that of the varieties of *Hippodamia* with confluence, as would be expected where intergrades are more frequent. The forms are inherited as if they represented an extreme in fluctuation, but

with this difference, that the confluence will crop up in some of the progeny nearly if not quite to the full degree. Even though there is segregation of the germinal representatives of these characters, fluctuation is so great as to obscure it. The explanation of these facts on the basis of blending heredity seems at first more satisfactory. The difficulty with that hypothesis is the failure of these variations to have long since disappeared by swamping. We may assume that variations in the direction of confluence are determined and that they continue to appear from time to time. Their failure to carry the whole species to a greater degree of confluence is probably checked by selection either in hibernation or through predaceous foes or by subponderance.

TABLE 19.—*Heredity in Epilachna borealis.*
[C. S. H.=Cold Spring Harbor.]

Father.		Mother.		2 and 3.			5 and 6.			5 and 7.		6.					
No.	off-spring of—	No.	off-spring of—	No.	Nor.	Approach.	Slight +.	+	Small intermediate spot.	Approach.	Slight +.	+	Approach.	Slight +.	+	Reduced size.	Free from suture.
C. S. H.	C. S. H.	243 ♀	C. S. H.	38	30	z	M
479 †	243	479 †	243	3	F M 3
C. S. H.	C. S. H.	237 ‡	C. S. H.	17	M 13½
C. S. H.	C. S. H.	208 ‡	C. S. H.	1	M 1
C. S. H.	C. S. H.	236 ♀	C. S. H.	24	19½
276 †	236	276	208	59	M 49½
348 ‡	243	348	243	5	2
201 †	C. S. H.	201	C. S. H.	1	M 1	F
300 †	C. S. H.	300 †	C. S. H.	11	M 5½	M
C. S. H.	C. S. H.	470 ♀	C. S. H.	48	2½	2
C. S. H.	C. S. H.	216 ♀	C. S. H.	2	1	M
C. S. H.	C. S. H.	267 ♀	C. S. H.	24	10½	..	1
C. S. H.	C. S. H.	470 ♀	C. S. H.	8	2½	2½

* The individual with 2 + 3 was 1 + 2 + 3 on one side.
 † Pigment along suture towards base in one.
 ‡ Both having 5 ap, 7 had 5 ap, or + 6.
 § Pigment along suture towards base in one.

Epilachna toweri n. sp.

Distribution: Texas (Comal County).

This species most nearly resembles *E. borealis* Fabricius. The pigment area is reduced, but along the lines of variation seen in *E. borealis*. The space between the two median spots on the pronotum is about one-half the length of the pronotum. The caudo-mesal spot is free from the caudal margin of the pronotum. The lateral pronotal spots are about one-fourth the length of the lateral part of the pronotum. The mesal spot of the intermediate row on the elytra is not confluent with the suture. So far as color-pattern goes, these beetles would not be given more than subspecific status. There is, however, a difference in form that is distinctive. The elytra are more convex, increasing the ventro-dorsal dimension. In the basal part of the elytra the slope is only slightly curved, as shown in fig. 89. The area between the two humeral spots is thus flattened and the

height of the elytra in the basal region is low. The elytra are also a little broader and the pronotum a little flatter. The ground-color is a lighter yellow than that of *E. borealis*. It is desirable to find if this species does not feed upon some other food plants than those of *E. borealis*.

This species is named in honor of Prof. W. L. Tower, of the University of Chicago, whose experimental work upon the genus is awaited with great interest.

Epilachna corrupta Mulsant.

Distribution: Arizona, Mexico, and New Mexico.

Typical pattern: Spots 1 and 4 are free from the suture and in place of a large single apical spot are 2 smaller ones placed well apart transversely.

Form A.

Mesal and intermediate spots of the intermediate row narrowly confluent; 1 specimen and some intergrades.

Var. *juncta*, n. var. The two apical spots confluent; 1 specimen.

The food plant is the bean. The larvæ refused to eat cucurbit leaves of several species. They were successfully reared, however, on bean leaves at Cold Spring Harbor. The imagoes showed no modification there in the direction of the pattern of *E. borealis*; in fact, a few showed a slight decrease in the amount of pigment. The attempt to hybridize them with *E. borealis* was unsuccessful.

Epilachna mexicana Guerin.

Distribution: Mexico and adjoining parts of the United States.

This species shows a reversed pattern, light spots upon a dark ground. Living specimens could not be obtained nor enough dead ones to make a study of the variation.

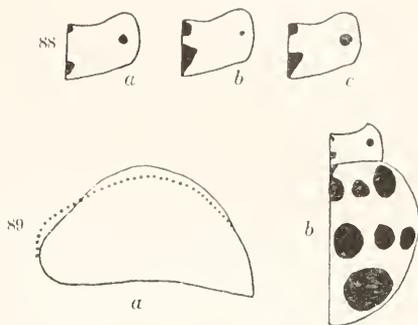


FIG. 88.--Variation in pronotal pattern of *Epilachna borealis* exposed to 40° C.

FIG. 89.--*Epilachna toweri*. a, comparative outlines of elytra from the side; solid line, *E. toweri*; dotted line, *E. borealis*; b, color-pattern of pronotum and elytra.

PART III.
GENERAL DISCUSSION.
VARIATION.

The variation in the color-pattern of these beetles is so great that the first impression is that it would be useless for taxonomic purposes. Some entomologists have on this ground ventured to say arbitrarily that color differences alone shall be an inadequate specific distinction. While this practice has the warrant that where only a color difference is found, the distinction is generally in fact varietal, such a discrimination against color is of course untenable when the two forms are a distinct unit which do not interbreed. On the other hand, Major Casey considers the color differences in this family of such taxonomic value that he has created many species thereon which others believe must be ranked as forms or varieties.

After an acquaintance with these beetles in large numbers, the variations are seen to have very different values. A considerable addition or loss of pigment at some places on the elytra or pronotum will be recognized as a mere fluctuation common throughout the range, whereas a very small amount of pigment at another point would show it to be a separate variety or even a distinct species. To the experienced coleopterist this is a commonplace, but the neglect of it by the Wallace-Weismann school of selectionists makes it worthy of note.

In general, the mere amount of pigment has the least significance. If this pigment is not evenly added to the spots, it becomes more significant. But if it is along the set lines for that species, it is of comparatively slight consequence. It is when it breaks out from the set lines to appear at a different point or to extend in new directions that the systematist may lay stress upon it.

That the variation is determinate is shown in many ways. By determinate variation is here meant a progressive variation in some definite direction, originating within the germ-plasm either with or without external influence, and gradually, by waves or by leaps. The progeny differ in the long run from the parents in some one direction, instead of offering indifferently plus (+) and minus (-) variations in all the old characteristics and having new characteristics in all directions, as seems to be assumed by Wallace and in the earlier writings of Weismann. I have not used the term orthogenesis, as I think that it is generally used for determinate evolution operating unswervingly and without divergence in one direction for a long period. Eimer thus used it, contending that the longitudinal pattern steadily and unflinchingly develops into a transverse pattern. It is not impossible that such phenomena exist, but the determinate variations here described can not be so characterized. Diversity prevails. Determinate variation will be working in several features at once, advancing now here and now

its structure. So, then, determinate variation in the direction of loss is widespread. That its evolutionary effect is not greater is the result of natural selection, because so great a difference as actual absence is more likely to have selection value than small differences, and because it is often opposed by the activity of determinate selection towards some constructive end. Thus in *Hippodamia convergens* variations of loss probably arise in regions where determinate variation is building up a pattern of confluence. Such negative variations would serve merely as a slight and easily surmounted obstacle.

This hypothesis makes it unnecessary to resort to such questionable hypotheses as use-inheritance or panmixia, to explain the decadence of unused organs such as the eyes of cave animals. If use-inheritance or panmixia be accepted to explain these cases, then no useless organ should persist. This persistence of some useless organs, such as the anal spine in some moth larvæ, offers no difficulty to the hypothesis of loss of determiners, for the frequency of this loss would depend on the nature of the determiner-complex and on the presence or absence of opposed lines of determinate variations.

It is not uncommon to find two spots which are confluent in some specimens showing in others, where there is no confluence, pointed extensions each directed toward the other. Such may be seen in many of the figures. It is abortive confluence. This indicates that confluence is not the pigmentation of a third unit, a connecting bar, between the two spots in question. It is rather an extension of pigmentation from the spot in a

KEY TO TABLE 20.

Anisosticta.	Hippodamia.	Adalia.
1. strigata.	15. cockerellii.	40. bipunctata.
<i>a.</i> var. bitriangularis.	16. dispar.	<i>a.</i> Var. herbsti.
Naemia.	17. parenthesis.	<i>b.</i> Var. quadrimaculata.
2. seriata.	18. apiculis.	<i>c.</i> Var. ———
<i>a.</i> Form A.	<i>a.</i> Var. $\frac{1}{2} + 3, 1 + 2 + 4$	41. frigida.
<i>b.</i> Var. litiginosa.	$+ 5 + 6 + a.$	<i>a.</i> Var. parvula.
Macronaemia.	19. americana.	<i>b.</i> Var. immaculata.
3. episcopalis.	20. sinuata.	<i>c.</i> Var. humeralis.
Paranaemia.	21. falcigera.	42. Annectans.
4. vittigera.	Neoharmonia.	<i>a.</i> Var. humeralis.
Megilla.	22. ampla.	<i>b.</i> Var. transversalis.
5. maculata.	23. ventusta.	Harmonia.
<i>a.</i> subsp. floridana.	24. notulata.	43. picta.
Ceratomegilla.	Coccinella.	<i>a.</i> Var. blanchardi.
6. ulkei.	25. johnsoni.	<i>b.</i> Var. concinator.
Eriopsis.	26. perplexa.	44. hudsonica.
7. connexa.	<i>a.</i> Var. subversa.	Agralia.
Hippodamia.	27. novemnotata.	45. cyanoptera.
8. glaciulis.	<i>a.</i> Var. franciscana.	Anisocalypta.
<i>a.</i> Var. <i>G.</i>	<i>b.</i> Var. confluenta.	46. duodecimmaculata.
9. convergens.	<i>c.</i> Var. californica.	47. quatuordecimguttata.
<i>a.</i> Var. obsoleta.	28. californica.	<i>a.</i> Var. ———.
<i>b.</i> Var. moesta.	<i>a.</i> melanocollis.	<i>b.</i> Var. ———.
<i>c.</i> Var. quinquesignata.	29. trispis.	Anatis.
<i>d.</i> caseyi, etc.	30. transversoguttata.	48. quindecimmaculata.
<i>e.</i> Var. 4.	31. monticola.	49. mali.
10. spuria.	32. diffeilis.	50. rathvoni.
<i>a.</i> Var. complexa.	33. prolongata.	51. lecontei.
<i>b.</i> Var. 1, 4 + 5, 6.	34. suturalis.	Epilachna.
<i>c.</i> Var. lineata.	Cycloneda.	52. borealis.
11. tredecimpunctata.	35. sanguinea.	<i>a.</i> Var. 1, 2, 3 + <i>r</i> , 4,
<i>a.</i> Var. signata.	36. munda.	$5 + 6 + r, 7.$
<i>b.</i> Var. spissa.	37. ater.	53. toweri.
<i>c.</i> Var. borealis.	Olla.	54. corrupta.
12. lengi.	38. abdominalis.	<i>a.</i> Var. juncta.
13. bowditchi.	<i>a.</i> Var. semilunaris.	55. mexicana.
14. oregonensis.	39. plagiata.	

definite direction. These extensions in the case of most spots are always true in their aim and meet each other exactly. In others, as *m* and *a* in *Coccinella*, the approach is ragged. In those beetles in which the black spots are all confluent one would expect, if confluence were the mere result of overgrowth of pigmented areas, that the light areas thus inclosed and remaining as clear spaces in their turn would have projecting points and concave sides. Such spaces are not wholly unknown, they are illustrated in one variety of *Ncoharmonia notulata*. But generally such lacunæ are rounded, giving rounded spaces with a black background. There must, therefore, be in this case a confluence by definite mutual extension of the spots.

These orderly extensions point conclusively to determinate variation. But since there is nothing in the structure of the elytra to explain why a spot should be here or there in the cephalo-caudal direction, it seems probable that the nature of the determiner-complex for the elytra must be such as to cause variation in these particular set lines rather than haphazard.

Asymmetrical specimens are not uncommon in looking over large series and are frequently sufficiently marked as to leave no doubt that they are the result of some inequitable distribution of the determining agent, whatever it be, in development.

That there are both fluctuations and mutations present in these beetles is probable. But under the name of fluctuations we group three different things. First, there are the modificational differences. Second, variations arise in spite of similar germ-plasm and similar environment, from the difficulty of constructing a soma according to the germinal specifications even with a similar environment. The developmental processes are not adequate to the task of producing exact fac-similes. Third, there are the variations resulting from slight germinal differences. Of these three kinds, only the third is inheritable. All three are to be found in these beetles. Their evolutionary significance is obviously very different.

MODIFICATION.

When a full-grown larva of certain species is subjected to certain influences which are maintained through a part of the pupal period, modification of the color-pattern results. But the portion of the color-pattern which responds differs not only with the influence employed, but also with the different species. Thus 40° produces no noticeable effect upon *Cycloneda sanguinea*, *Coccinella novemnotata*, *Megilla maculata*, and *Hippodamia convergens*, nor upon the elytra of *Epilachna borealis*. But the pronotum of the latter has its pigment very much reduced; in fact, in some specimens, to the degree of reduction found in the Texas species *Epilachna toweri*. Refrigeration does not affect the pigmentation of the elytra, but increases the pigment of the pronotum, though not to a degree comparable to the reduction of pigment by heat.

In the *Hippodamia convergens*, on the other hand, both pronotum and elytra have the pigment increased by the same degree of cold and uninfluenced by the same degree of heat. The use of various other influences on these and other species produces no effect. Modifiability of this or that feature is then itself a characteristic. It is a characteristic sometimes gained and sometimes lost, sometimes always firmly coupled with the feature in question, and sometimes never possessed by it.

The result has been spoken of as increase and decrease of pigment. We have seen that this may not apply at the same time to both pronotum and elytra. Even in one organ, while modification manifests slight influences merely in the diameter of the several spots or marks, with a stronger influence the additional pigment is laid down in certain directions rather than in others. The result is that the pattern is not merely darkened; it is changed.

The interesting question arises, Are these changes identical with hereditary changes in phylogeny or something quite different? Some are clearly identical, such as the lateral process of the pronotum of *Hippodamia convergens*, and some are clearly different from any hereditary condition known, as shown in fig. 26.

If we examine these two categories carefully, a generalization is possible. The influence of structure is frequently obvious in characteristics which are the result of modification, much less frequently so in hereditary conditions. In modification, pigment follows the veins and the margin to a much greater degree than in inheritance, where some characteristics are wholly free from the influence of somatic structure, such as the spot *q*. Of course this is just what should be expected. It is the opposite condition, where the hereditary and modificational changes are the same, several cases of which have been shown in Part II, that calls for discussion.

The most acceptable explanation is that the directing protoplasmic elements in the developing somatic cells have so much in common with the protoplasmic elements in the germ-plasm that both are similarly affected. If we assume this, some important corollaries follow. An environmental influence may affect the soma and the germ-plasms simultaneously, so that in the following generation there is the same effect as would have taken place if there had been an inheritance of an acquired (somatogenic) character. Such phenomena as this are, I believe, not uncommon, not only in the evolution of these beetles, but very generally. Indeed, recent neo-Darwinian writings are making greater and greater concessions to this view. The advocate of the inheritance of acquired (somatogenic) characters must show the inheritance of a character which is incapable of affecting the germ-plasm in the same way as it affects the soma. These are particularly the kinetogenetic characters. The neo-Lamarckian may well contend, however, that the admission that the germ-plasm is influenced by the environment in such a way as to produce definite evolutionary

results constitutes a far-reaching compromise which goes far to justify the faith he has placed in the rôle of environment.

The fact that some characteristics are never inherited, but are always mere modifications, and that others are wholly free from the influence of modification, has a practical bearing to the systematist and to the breeder. The systematist would do well to determine experimentally, where it is feasible, which characteristics of those he deals with are especially subject to modification, by the differing influences of season and range. Such will be his "poor" characters for species distinction and important ones for subspecific distinctions. The breeder will find that characteristics especially subject to modification must be subjected to as uniform conditions as possible, whereas this effort may be saved with other characteristics.

The modifiability of *Hippodamia convergens* suggests that some of the sub-species in this family might be merely ontogenetic in origin, but this is doubtful, for all that I have brought to Cold Spring Harbor and bred there have retained their characteristics. The variety *moesta* would naturally be most subject to suspicion on this score, but it is found on the outskirts of its own range in company with beetles which are even spotless and yet without any loss of its typical character. Any rigorous attempt to modify the germ-plasm, as accomplished by Tower (1906) in *Leptinotarsa*, requires the subjection of large numbers under elaborately controlled conditions. It is not surprising, therefore, that my attempts, which fell short of these conditions, gave negative results when they did not result in death. Still, I believe from the facts of variation and distribution that some such germinal modifications as those in *Leptinotarsa* might be produced, but probably in a much smaller percentage of cases. Our interest here is primarily in the imaginal coloration. Yet the far greater modifiability of the pupal coloration, when the prepupa is exposed, is worthy of remark. The pupal exuviae of *Epiplatna borealis* varied from colorlessness, except in the spines in the heat experiments, to a highly pigmented pattern of stripes and other marks in the cold experiments described.

DISTRIBUTION.

If the view here entertained of the importance of the direct action of the environment is correct, the task of unraveling the dispersal of a species becomes more complicated. The criteria of Adams and others would be less reliable in their application. The four criteria acceptable to Tower (1906) of the considerable number that have been proposed by which the center of dispersal can be located are as follows:

- (1) Location of greatest differentiation of a type (Adams).
- (2) Continuity and convergence of lines of dispersal (Adams).
- (3) Location of synthetic or closely related forms (Allen).
- (4) In some cases, location of dominance or great abundance of individuals (Adams).

By the first criterion the Pacific States would be the center of origin of *Coccinella trifasciata*, but this seems to me the least probable center of origin. In all other localities this wide-ranging beetle is constant to a pattern which is present in other species. In the Pacific region it yields to the general tendency there and gives a series of variations towards reduction. The conditions of the criterion are thus fulfilled, but the conclusion does not follow. The position of greatest differentiation is not only a result of time, but also of the diversity and efficiency of the environmental influence.

The fourth criterion of great abundance is so obviously in the control of the environment and subject to such rapid changes that it is not of aid here.

Multiple origins must be reckoned with. When the environment is capable of producing changes of the germ-plasm, we may expect similar changes to take place independently throughout the one unit of environment and in other disconnected but similar environment units. *Hippodamia convergens* would probably give rise to var. *quinquesignata* wherever it encountered mountains in the same general region.

There is a great wealth of varieties of *Hippodamia convergens* in the Western States in contrast to a uniform monotony in the Eastern States. The criteria of dispersal would lead us to conclude that the Western States were the center of dispersal, but I think this is not justified. *H. convergens* "flies to pieces" in that region. It would do so at the time of origin if it arose there or at time of entrance into it, if it arose elsewhere.

We are, then, reduced to a very cautious use of criterion 3 with slight aid from criterion 2. The results are not sufficient to make it possible to reconstruct the dispersal of any species from those here studied, and only one reasonably safe conclusion appeals to me.

Coccinella novemnotata var. *menetriesa* and *C. transversoguttata* are common to eastern Asia and western America. There is a close relation between *Hippodamia amoena* of Siberia with *Hippodamia apicalis* of Western America and between *Coccinella mannerheimii* and *Coccinella tricuspis* and between *Cocinella interrogans* and *Cocinella sinuata* of Asia and America, respectively. Species common to Europe and North America are found in Siberia as well, with the possible exception of *Adalia bipunctata*, which Leng suggests was introduced into North America. These considerations would lead us to believe that the latest route of dispersal between the Palearctic and Nearctic realms was by the Aleutian or Behring route. I do not believe that we are justified in concluding at present in which direction the greater amount of dispersal took place.

One expects the different species in a region to occupy different niches in the environment. This at least is a corollary of the current belief that every species is as common as it can be, its numbers being limited only by its food-supply, a belief which is the result of the strong Malthusian leanings of Darwin. The major species of the coccinellids do not seem to be

so distributed. With certain exceptions which we have given, the species of *Hippodamia* and *Coccinella* are in quite general competition. They are characterized for the most part by very wide distribution and extensive overlapping of other species. With the exception of a few species like *Cleis hudsonica*, there is little zonal distribution. The apparent zones of distribution, as given for New Mexico by Cockerell (1898), are in marked disagreement with other regions.

The abundance of the several species is also very erratic from place to place. At Cold Spring Harbor the order of abundance of the several species differs from year to year and is quite different from that given for other localities not far distant. The conclusion seems evident that the exigencies of the death-rate are great and that these species have difficulty in leaving 2 progeny for each pair, not because of overcrowding, but from some other unfavorable circumstance. Small considerations, such as the activity of some disease of aphids here or there, turn the balance against this or that species, though it may be in the middle of its range. If this be the case, then just such wide overlapping ranges should be found. The distribution of the varieties as opposed to that of the species must be separately considered, for here we have different conditions. The facts of the varietal distributions apply also to some species of a narrow range which are closely related to some species of wide range and which are more or less certainly derived from them at a relatively recent date. These are young species not far removed from varietyhood and, not unnaturally, distributed much as varieties are. They will be distinguished as minor species in distinction from major species.

In *Hippodamia*, especially, we have wide-ranging major species. Sometimes on the outskirts, sometimes on the interior part of its range, are found the lesser ranges of the varieties and minor species. This is illustrated diagrammatically in fig. 91 for *Hippodamia convergens* and its derivatives. Such a distribution is, I believe, very significant in the study of evolution in this group. It points strongly to the directive influence of the environment and to the rôle of segregate heredity in the evolution of a species up to the varietal stage, at least, within the territory occupied by the mother species. The difficult step by which the variety acquires intersterility and thus becomes a species must be discussed in a later section.

When the new species has arisen, the extension of its range, as we have seen, is not checked by any coccinellid saturation of the environment, and depends largely upon the degree of success it has in the distribution of its eggs and in its success in hibernation. If relatively successful, it takes its rank as a major species; if less so, it continues as a species of narrow range; if still less so, it continues as a rarity which persists, in spite of its high death-rate, through the mass of recruits constantly furnished by the mother species.

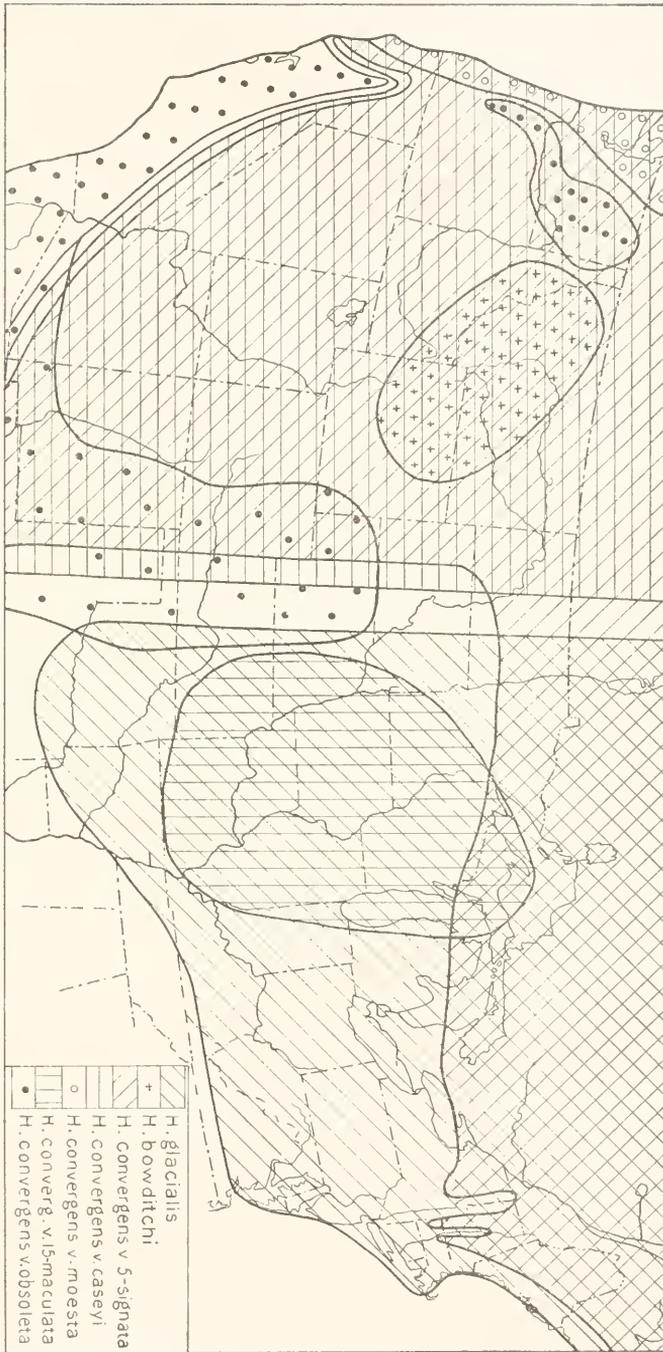


Fig. 31.—Distribution of some derivatives of *Hippodamia convergens* in the United States (diagrammatic).

David Starr Jordan has proposed a law of distribution of great value, not because it is universal, for it is not, but, still better, because it is to some degree indicative of the nature of evolution in the species considered. "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." President Jordan has subsequently stated that "barrier" is here used in a very broad sense. This law gives the state of affairs that we should expect if evolution were mainly the work of isolation and were taking place by even flow rather than by waves or mutations. It is doubtless mainly his knowledge of the distribution of fish that led President Jordan to this formulation. Its applicability to the vertebrates is quite wide. Botanists do not seem to find it of as general applicability in plants; indeed, in some genera, like *Draba*, the opposite condition prevails. In invertebrates but few authors have considered it. It is important that many groups should be examined with this in view, for it throws valuable light on the method of evolution. We have seen that it is largely inapplicable for the major species because of their extensive overlapping.

For the consideration of the distribution of varieties and minor species I have drawn the distribution of the several derivatives of *Hippodamia convergens* in fig. 91. The distribution of *Hippodamia convergens* itself is not shown. It is found throughout the area of the map. It will be seen that Jordan's law fails here, for the closest allied forms occupy the same region in all cases with the parent species and in many cases with an allied variety. Thus the closely allied variety *quinesignata* and variety *caseyi* have ranges nearly coextensive in the west. So far as our data goes, variety *caseyi* does not share the eastward extension of variety *quinesignata*. It is characterized by the possession of three of the four distinctive characteristics of the variety *quinesignata* and is so generally associated with it that I believe future study in the eastern mountains will reveal its presence. *Hippodamia bowditchi* dwells in a part of the range of its nearest ally and is surrounded by it. The conclusion seems inevitable that we are dealing here with systematic units that have not arisen by an en masse evolution of all individuals in the locality, but have arisen at first in a few individuals which by virtue of some degree of segregation in heredity have escaped being swamped. This conclusion, reached from the study of the distribution, is the same as that which the study of the variation and heredity of these beetles leads to.

Geographical isolation does not act in these beetles as the initial cause of separation as it does with blending characteristics. It may assist the variety in its progress, however, (1) by preventing too wide outcrossing and thus causing the individuals of the variety to more frequently interbreed, and (2) by helping the variety to attain intersterility and thus a specific status, in a way shown later. Specimens of *Hippodamia spuria* isolated from its close ally, *Hippodamia interrogans*, are more alike in gen-

eral in their color-pattern than are the extremes of *Hippodamia spuria* where there is no isolation.

Taylor (1894), Matthew (1908), and Cockerell (1908) have proposed the view of an "active evolutionary center" at which a genus or a higher group has reached its highest development and from which the new species arise and are dispersed. In this way the oldest species are found at a distance from the center. We do have an active evolutionary center for *Hippodamia* in the Plateau and Pacific States, but it is doubtful if the varieties of species there produced are dispersed and replaced. They are, for the most part, endemic and have no power to extend their range greatly into conditions quite different from those of their origin. Furthermore, the active evolutionary center is here caused by conditions of the environment capable of altering the germ-plasm rather than by any "intense pressure and competition there," as Taylor asserts of the active evolutionary center of the land snails.

HEREDITY.

In spite of the many non-conformable cases presently to be mentioned, many biologists have come to expect Mendelian segregation and dominance whenever segregate inheritance is found, so eagerly does the mind welcome and embrace any conception of uniform action. In the discussion of the several species we have seen that in only one case do the facts seem conformable where, as in several cases, they fail to conform to the simple Mendelian conceptions in spite of the fact of there being some degree of obvious segregation. For the biologist whose predilections are strongly Mendelian this is of little moment, for he will believe that these cases simply demand a few consistent hypotheses of additional factors, enzymes, inhibitors, coupling, latency, etc., to become quite conformable. Since a rigorous test of most of these subsidiary hypotheses to Mendelism demand very large numbers, greater than are often available in animal experimentation, the test is not be made and consequently his comfortable faith remains undisturbed.

But is it good scientific method to keep protected in this way the faith in the Mendelian behavior of insect characteristics? When we consider the results of Kellogg upon silkworms (1908), Lutz upon *Ampelophila* (1908 *c*) and upon *Grioceris* (1908 *a*), McCracken upon *Lina* (1907) and upon *Gastroidea* (1906), and Tower upon *Leptinotarsa* (1906), we find no genus in which there are not such un-Mendelian things as "individual and strain idiosyncrasy," "variation of allelomorph potency," "weak factors," "bilateral opposition of characters," "gradual elimination of alternative characters," "progressive dominance," and "inability to hand on variations with full intensity."

The least we can do is to give a fair consideration to hypotheses which seem to arise simply from the facts, for, as Chamberlain has well pointed out, the use of multiple hypotheses is a great safeguard to the soundness of scientific progress.

The hypothesis which seems to me to satisfy best the facts of heredity here and to be consistent with those of variation and distribution in these beetles is that of characteristic prepotency. Since the word "prepotency" is used in speaking of an individual, I would propose the term "preponderance" for the prepotency of characteristics. It is necessary to distinguish this from dominance. In dominance without the aid of selection there is no gain in numbers, since there is no germinal advantage with the dominant characteristic. In preponderance there is a germinal advantage, so that the characteristic gains in numbers without the aid of natural selection or even conceivably in opposition to it. In a character with blending inheritance, preponderance shows itself by the progeny resembling in the long run one of the two opposed characteristics more than the other.

In segregate characteristics it may show itself in the guise of hyperdominance, that is, by the numbers of the dominant characteristic being excessive, or in a differential tainting of the extracted homozygotes. Cases that seem to be more easily explained by resorting to preponderance (or subponderance) are the deficient proportions of most of the elementary species of *Oenothera* where crossed with *O. lamarckiana* (de Vries, 1901), the deficient proportions of abnormally veined *Ampelophila* when crossed with the normal (Lutz, 1907), the deficiency of polydactylism when crossed with the normal in man (Davenport, 1904), the excessive proportion of booting in booted \times bootless in poultry (Davenport, 1906), deficient proportion of the all-black *Lina scripta* \times normal (McCracken, 1907), excessive proportion of spotted *Lina scripta* in *L. scripta* \times black *L. scripta*, and excessive proportion of black *Gastroidea dissimilis* in black \times green (McCracken, 1906).

Many breeds of animals have what are called "faults," which are the distress of their breeders. These faults are sometimes merely the normal traits of the wild species or ancestral variety from which the variety is obtained, and their persistence would not be a serious problem except that the breeder is trying to handle so many characteristics. There is a greater degree of persistence in some, however, that can not be thus explained. Of recent years, these have been explained as the products of the meeting of heterozygotes which reveal recessive characters which may not have been seen for several generations, because the heterozygous individuals had not mated before. This is sometimes true without doubt, but in considering these cases from Leighton (1907, p. 321), and Simpson (1903, p. 117), the hypothesis of preponderance may well be considered. Here the preponderance shows by the difficulty with which the characteristic is submerged.

"Litters [of the white English terrier] frequently show the blemish of a spot of brindle or russet. These spots usually appear behind the ears or on the neck and are of course a disfigurement on a dog whose coat to be perfect should be white." This breed was quite popular at least 40 years ago, and any color or marking disqualifies.

“In most black litters [of black Persian cats] at least one has a white spot on chest or throat, and this generally settles the question which, if any, shall join the majority at a tender age. The unfortunate kit's pedigree may be absolutely devoid of offense on this point. Apparently no precautions can prevent or eradicate the fault.”

From the instability of some characteristics we may infer that they would be subponderant in heredity. Thus in Leighton, page 403, referring to the Dandie Dinmont terriers, we find the following: “It is generally best to mate a mustard to a pepper to prevent the mustards becoming too light in color, though two rich-colored mustards may be mated with good results.”

On page 87, “When brindle Great Danes are continuously bred together it has been found that they get darker and that the peculiar striping disappears and in that case the introduction of a good fawn into the strain is advisable. The constant mating of harlequins (black spots on white) has the tendency to make the black patches disappear and the union with a good black Great Dane will prevent the loss of color.”

The tendency of most white breeds of poultry to become cream-colored and of Barred Plymouth Rocks to become “smoky” asserts itself whenever selection of a good strain ceases. The stalwart Mendelian, in this last case, has an explanation in the assumption that “smoky” Barred is a unit-character, and that light Barred is only produced by the selection of fluctuations and hence must inevitably fall back when selection ceases. But this is nothing more or less than the assumption of the preponderance of the type of the unit-character over its derivative. The stalwart Mendelian then admits preponderance in fluctuations so long as they lead to a unit-character. If, then, there is nothing intrinsically impossible about preponderance, the only objection to it as a factor of evolution to the Mendelian lies in his conception of clear-cut unit-characters having a perfect segregation. Any belief in such sharply-cut phenomena is untenable in the consideration of the color-pattern of these beetles, where some degree of segregation is nevertheless positive.

Cases of mass reversion are, to my mind, often the result of preponderance of the reverting character over the newer conditions. Of course reversion taking place in cases following the cessation of short, active selection is to be attributed to regression.

The degree of segregation in heredity is most perfect in spots 1-3 in *Hippodamia convergens*. It varies by easy stages to cases in which the heredity is nearly if not quite blending, as in the relation of 5 and 6 in *Epilachna borealis* or as in the incomplete pronotal margin or in the size of the pronotal dash in *Hippodamia convergens*. Just short of blended inheritance we have such cases as those in which the bulk of the individuals lie between two extremes, at each of which many individuals are massed. The result may be likened to the balls on a bowling alley, which, while passing frequently the position of each pin, yet in the long run pass more

frequently into the side-gutters than any other one place. Only a suggestion of segregation is seen in 5 and 6 in *Epilachna borealis*. Here we see a variation curve strongly skew in the direction of confluence of spots, and the experiments in heredity give us progeny which seem for the most part intermediate, but nearly always there are many without confluence and some with fully as much or more than the parent. Here, then, confluence is not swamped, because, in spite of the majority of intermediate and normal progeny, a mechanism, in some ways suggestive of that which produces de Vries's ever-sporting varieties, maintains the supply of these confluent individuals.

In *Coccinella novemnotata* we have a type of heredity that deserves further mention. Here the variation consists of a series of steps. We have 4 spots in which we may have no confluence, or confluence of 2, of 3, or of 4 spots. Intergrades exist in which there is an approach to confluence or partial confluence; nevertheless the steps referred to constitute centers of variation more frequented than intermediate conditions. Now, the progeny may belong to the centers of variation of their parents, but also to the other centers. The variation is, then, moniliform and the heredity polymorphic.

The facts of variation and distribution in these genera show us that the swamping influence of intercrossing is not effective upon a large number of varieties. This immunity is obtained by some degree of segregate heredity. Absolute segregate heredity is not found, hence we may conclude that a variety may be protected from swamping by an only partly segregate heredity.

PHYLOGENY.

It is desirable if possible to decide upon the primitive pattern from which the coccinellid beetles were descended. Schoeder, while admitting that the pattern of *Adalia bipunctata* and its varieties are referable to a scheme of 7 spots and a scutellar mark, contends that the primitive pattern was one of vittæ. This was followed by barring, and a reduction of the network thus formed left the points of intersection as spots.

That the primitive pattern was one of vittæ may be possible if we go back to a sufficiently remote time. It is possible that coccinellids having as regular vittæ as those of *Paranaemia vittigera* have retained this pattern, with possibly some reduction in the number of vittæ. Tower (1906) finds that vittæ in *Leptinotarsa* are between the veins, yet the extension of pigment along the veins in modification experiments in the lady-beetles makes it possible that the vittæ were here differently placed. In *Adalia* these spots are upon the veins, but this can not be said to be the general rule. The position of the spots seems to be remarkably independent of the veins. The influence of the vein is much more evident in projections from the spots along the linea externa in *Coccinella novemnotata* and *Harmonia picta*.

The term "primitive" is a relative one and, in the working out of the evolution of the color-pattern, much more value lies in the ascertainment of the ancestor of the genus or subgenus than of a more remote ancestor. There are not enough data at present and there probably never will be to make the attempt to study the evolution of the color-pattern from genus to genus profitable, and this is not attempted in this paper. The study of evolution is served better by concentration upon the evolution of the pattern within the genus, subgenus, or species, and this has been my task. The distribution and number of spots differ in the different genera. These differences I believe have arisen by the different ways in which the vittæ have given way to spots in the phylogeny of the genus.

The beetles of each genus, with a few exceptions, where the unit is a subgenus, are referable to one set of spots. They constitute a pattern-unit. Within this pattern-unit the work of evolution is principally the loss or confluence of spots. Only rarely are new spots added. Change or shape of elytron sometimes shifts the position. Otherwise the position is very conservative.

The reasons for believing the spotted pattern to be primitive for *Hippodamia* at least are (1) the wide distribution of the spotted species, and (2) the narrow distribution and varietal nature of so many of the forms which have deviated from the spotted condition. But so difficult is the change of number and position of spots between the several genera that it is easier to conceive of them arising by independent origins from some primitive vittate condition.

EVOLUTION.

We have seen, in the preliminary discussions, that natural selection must be very feeble in the evolution of the color-pattern of coccinellid beetles. Since the pattern is for the purpose of association with the bad taste, if it has a purpose, its highest utility would lie in constancy and idiosyncrasy. The spotted pattern being in these beetles the commonest and characteristic one, natural selection, in so far as it is operative, should favor this pattern. If, then, we find any evolution away from this pattern, it must have taken place either without the aid of natural selection or in opposition to it. There is occasion for some doubt as to the primitive pattern of some of the genera and species. Let us consider, then, a case where the evidence that the spotted pattern is ancestral is conclusive, viz, *Hippodamia convergens* and its varieties. Here we have a species with the same spotted pattern that is possessed by several other species of the genus and which is widely distributed. In this beetle the spotted condition gives way to marked deviations from its original spotted condition in several ways in different varieties (fig. 11).

The question is, What has caused this evolution? Recourse to natural selection is debarred. The inheritance of somatogenic characters is open to such grave questions about the conceivable mechanism as to be very

doubtful. It is clearly inadequate to produce characters like the *extensa* mark or the spot *q*, which environment could not produce acting upon the soma alone. Further, many of the somatogenic characters do not become germinal, as the dark linea externa in *Hippodamia convergens*. On the other hand, we have seen, in studying the variation and heredity of the markings, evidence of determinate variation and of preponderance. It is to this first factor, aided, I believe, by the second, that this evolution is to be attributed. Since their action is analogous, I have grouped them under the name of determinate evolution in the title of this paper.

Determinate variation is a dual process, for although the environment frequently causes certain variations, as will be shown later, the nature of the germ-plasm is a more important element in determining whether there shall be any variation formed and what it shall be. In other cases the environmental control of the germinal change is so minor a feature that it is negligible and the cause may be said to lie in the nature of the germ-plasm. The relative rôles of environment and the constitution of the germ-plasm are interesting in the case of disappearance of spots, where we found in one environment one spot especially disposed to disappearance, whereas in another environment it is another spot (fig. 17). The rôle of the environment is shown in the following cases: On the Pacific coast, outside of the mountains and the humid coast region, there is a strong tendency to disappearance of spots, five species yielding to this tendency. In the mountains, transverse confluence reigns. In the humid Pacific coast region *Hippodamia convergens* gives us the very dark variety *moesta*. It is possible that marshes evoke vittation, for *Hippodamia sinuata* (*trivittata*) is a marsh-dweller, as is *Paranaemia vittigera*, while *Naemia seriata* is maritime; but this must be further investigated. Arid regions lead to the reduction of spots, although the greatest proportion of spotless individuals is not found in the region of greatest aridity.

Where two species are affected by one of these environments, we should get corresponding results. This is realized in the Cascade Mountains, where we have the barred *Hippodamia oregonensis*, a derivative of *H. spuria*, and the barred variety *quinqesignata* from *H. convergens*. In the Hudson Bay region, with the vittate *H. falcigera* we get the vittate derivative of *H. tredecimpunctata*—the *Hippodamia americana*.

In the Pacific coast region outside of the mountains and in the humid region, spotlessness is found in *Hippodamia convergens obsoleta*, *H. tredecimpunctata* var. *immaculata*, *Coccinella perplexa* var. *subversa*, *Coccinella noremnotata* var. *franciscana*, and *Coccinella californica*, probably a spotless derivative of *Coccinella transversoguttata*. Yet it should be mentioned that *Hippodamia parenthesis*, *apicalis*, and *spuria* resist the general trend towards spotlessness.

The rôle of the environment must not be overemphasized, for its part may be likened figuratively to the heat that starts a chemical reaction. Where heat is applied, the result differs with the different chemicals

affected. No reaction may result, comparable ones may result, or wholly different ones may result, and besides, different degrees of the heat may be necessary to give any of these results.

Adalia bipunctata in Europe has many varieties, modified in the direction of greater pigment, and many of them are found in any one locality (Weisner, 1907), yet in America this species is relatively constant. *Coccinella perplexa* and its very close European ally, *C. trifasciata*, with an elytral pattern practically identical, are quite constant, except in the Pacific States, where there are many varieties of reduction. *Hippodamia parthenesis* maintains a greater constancy in the Western States, where so many species become especially prolific in varieties than it does in the Eastern States.

In the Eastern States most of the species do not find the conditions such as to set up new variation lines. Yet *Coccinella novemnotata* gives us its varieties of vittation in the East, and throughout the Plateau and Pacific States it offers no varieties but those of reduction. *Megilla maculata* and *Naemia seriata* suffer reduction of spots in the Southwestern States, where the other species are also thus affected. *Hippodamia apicalis* suffers a greater reduction in Eastern Colorado than in the Pacific region.

Determinate variation governs the birth of a variety, but its later career is governed largely by its method of inheritance and by natural selection. If the variety is subponderant, it will probably take the status of a rarity, arising again and again by the determinate variation but never winning an important place. It is possible that subponderance in some characters is capable of being converted into preponderance by selection or by the action of environment on the germ-plasm and a place thus acquired by it. In others their subponderance may be expected to be fundamental and unalterable. If the characteristic be preponderant, its way is made smoother, and if determinate variation cooperates by frequently offering the variation, the characteristic is sure to make its way unless opposed strongly by natural selection. If it arises very rarely, its fate is in jeopardy. A mutation which arises only once has a very small chance of success. The frequency with which it arises is an important element in its fate.

This analysis is carried further in table 21. We see, in examining this table, why a variety aided by determinate variation does not always supplant the species, but often reaches a status of a certain degree of relative abundance which it may retain for a long time. Thus in Oregon the variety of *Hippodamia convergens* with open pronotum continues to exist as a rarity, avoiding extermination on the one hand and increase on the other, because it is kept in existence by determinate variation, and, as I believe, is kept repressed by its subponderance. Since the activity of natural selection, determinate variation, and preponderance are each found in

various degrees, the categories used in the table are of course not sharply limited, but merely arbitrary points taken for exemplification.

There can be no one general orthogenetic influence here, so diverse are the many varieties which have arisen from *Hippodamia convergens* in different regions. Eimer's law, that a primitive pattern of stripe is followed by spots, which in turn give way to transverse striping, and last of all to a uniform color without spots or stripes, can not hold. In fig. 90 the varieties of *Hippodamia convergens* are so arranged as to show how one degree of one line of development may be combined with another degree of another line of development. In fig. 29, in *Hippodamia spuria*, a similar condition is met with, even though here we deal with both stripe and bars. Another law of Eimer's, "new markings appear upon the body of an animal from behind forwards and above downwards, or conversely, whilst the old ones disappear in the same direction and succession," is also untenable. The study made of the order of disappearance of spots does not bear out this rule, nor does the appearance of new spots, such as *q* and *e* in *Hippodamia convergens*, conform to it. The diversity of patterns here makes impossible the formulation of any general orthogenetic law, for, as we have seen, they progress differently from place to place. In fact, the general diversity of the animal kingdom throws great doubt on all general laws of orthogenesis. The doctrine of determinate variation is only handicapped by the formulation of these rules, which must be so soon abandoned. Determinate variation is as multifarious as are the phenomena it aims to explain.

TABLE 21.—*Effects of cooperation or of opposition of some evolutionary factors upon a new characteristic.*

Natural selection—	Heredity subponderant.		Heredity indifferent.		Heredity preponderant.	
	Variations arise relatively very infrequently.	Variations arise relatively frequently.	Variations arise relatively very infrequently.	Variations arise relatively frequently.	Variations arise relatively very unfrequently.	Variations arise relatively frequently.
Opposes.....	Remains extremely rare.	Remains rare.	Remains very rare.	Remains rare.	Doubtful result.	Doubtful result.
Indifferent.....	Remains very rare.	Remains rare.	Remains rare.	Remains uncommon.	May increase.	Increases.
Favors.....	Doubtful result.	Doubtful result.	May increase.	Increases.	May increase rapidly.	Increases very rapidly.

Evolution may conceivably proceed in a regular and continuous fashion, and it has been generally so conceived, until of recent years, when much attention has been paid to the evolution by leaps. Considerable evidence, as to positions of organic stability and unit-characters, is held to substantiate this view. In these beetles we would seem to have both saltatory evolution in a character like 1 + 3 in *Hippodamia convergens* and evolu-

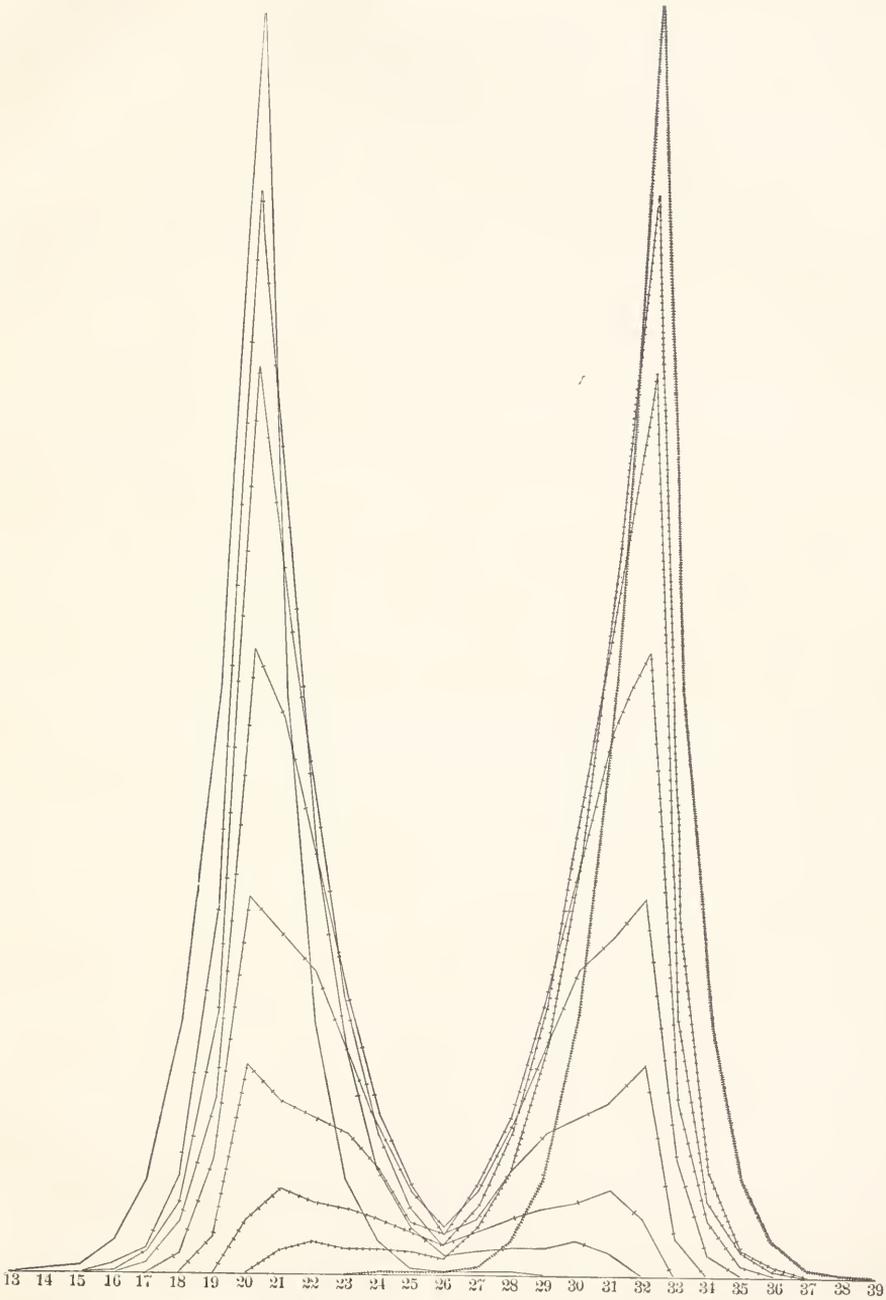


FIG. 92.—Hypothetical polygons to illustrate centers of variation and evolution by waves.

tion by even flow in the lateral process of the black area in the pronotum. But, in addition to these, I believe we have a third intermediate method, evolution by waves; for most of the characters, while showing some degree of discontinuity in variation and segregation in heredity, are not so discrete as to be properly called unit-characters. They are better described by Galton's expression "positions of organic stability," interpreting position in a broad sense. I prefer the expression "centers of variation." Thus, in the size of spot 1, instead of two unit-characters at 5 and 15 units diameter, it seems to me we have more probably two centers of variation at these two points. This distinction would be of little importance were it not for some important evolutionary consequences.

The centers of variation (and here I am not speaking of the clear-cut cases of unit-characters) may be the result of either of two possible causes. In one kind, the germinal centers of variation, the positions of organic stability are those of the germ-plasm, depending upon the nature of its structure and processes. In the other kind, that of somatic centers of variation, we have positions of organic stability of the soma, the germ-plasm in this case not showing any corresponding favor for one degree rather than another. We may illustrate this latter type by considering the evolution of a pattern from one in which two spots are separate to one in which they are confluent. It seems to me not only possible but probable that it is easier for the spots to develop separately or in full confluence than with a narrow connecting band. Now, as the determiners move on in the direction of confluence (whatever may cause the movement), individuals which have intermediate determiners will be more likely to have the confluence either less or more than that determined by the germ-plasm. The result will be a bimodal polygon of frequency, until the germ-plasm has progressed far enough to carry all the individuals past the position of disfavor.

In fig. 92 I have aimed to illustrate this in a hypothetical case. For the polygon of frequency I have taken the one used in Davenport (1904) to illustrate the normal curve. Now, I have assumed arbitrarily that the magnitude 20 of the character is a position of organic stability, being favored at the expense of other magnitudes to the extent that it receives eight times as many individuals as it would otherwise receive; that the neighboring classes are favored fourfold; those next adjoining twofold; those next are unaffected. The next three classes are reduced to the extent of getting only one-half, one-quarter, and one-eighth, respectively, of their quota. The numbers thus obtained have been reduced to percentages. The polygon of frequency centered over 20 with the changes thus produced is shown as the first position in table 22 and fig. 92. Now, let the character evolve by the increase of the magnitude by any factor of evolution. The polygon will move to the right and assume the successive positions shown in table 22. In fig. 92 these curves are graphically represented, with a few omitted to avoid overcrowding.

the species, and since var. *caseyi* has arisen within the range of *H. convergens*, this seems to be the most probable explanation, especially since the color-pattern difference is correlated with a difference in size, as shown in table 10.

Where isolation can be resorted to, an explanation is simple. Determinate variation in the isolated groups has worked in different directions, so that the reproductive organs or processes may have often become so diverse as to make them intersterile if a breakdown of the isolation brings them to the test. In this I would suggest we find a reason why great organic differences in artificial varieties do not bring about intersterility, while much slighter differences in nature do. In the latter case determinate variation has had its opportunity; in the former it has not. In these beetles, however, isolation can only rarely give this assistance.

SUMMARY OF CONCLUSIONS.

(1) *Variation*.—Both continuous and discontinuous variations are found in the color-pattern of these beetles. Variations are also found disposed around certain centers of variation in greater numbers. Yet these centers lack the discreteness necessary to constitute them unit-characters.

(2) *Modification*.—The color-pattern is capable of modification by the environment. Some modifications exist as hereditary characters also, while others do not. Non-hereditary modifications are more controlled by the structure than are the hereditary variations. The germ-plasm and the soma are in some cases capable of parallel modification, thus producing an apparent inheritance of somatogenic characters.

(3) *Distribution*.—The species overlap to a great extent. The varieties occur with the typical species in a part of their range. Jordan's law is in general not followed; hence the evolution is probably for the most part not by the even flow of all the individuals in a region.

(4) *Heredity*.—Segregate (alternative) heredity is general, but it varies by degrees from blending to a typical segregate heredity. Mendelian interpretations meet with difficulties in most cases. It is probable that we have preponderance (prepotency of characters) in some cases.

(5) *Phylogeny*.—There does not seem to be adequate ground for postulating a definite single pattern as the primitive one for the family. Eimer's laws of pattern development are not applicable. Several congeries of varieties or species of diverse patterns may be attributed to descent from a spotted pattern.

(6) *Evolution*.—Natural selection, if at all active, is principally conservative of the spotted pattern. In spite of this, determinate variation, largely actuated by the effect of the environment on the germ-plasm, and probably preponderance as well, have accomplished marked evolution of the pattern from this condition. Evolution proceeds by waves as well as by even flow and by mutation in different characteristics at different times.

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