INHERITANCE IN LADY BEETLES

I. The spotless and spotted elytra of *Hippodamia sinuata**

A. FRANKLIN SHULL

THE great variability of the patterns of lady-beetle species has attracted the attention of naturalists for many decades, and invited speculation concerning its significance in evolution. Evidence of genetic segregation was observed at least as early as the closing years of the last century, but not always so interpreted. The black variety of *Adalia bipunctata,* sometimes labeled a species of *Coccinella* in the early collections, was crossed by Burgess[1] with the normal red form, and both types appeared in the progeny. Although the female might not have been virgin in this first cross, the fact that the male possessed the rarer character and that this character was borne by some of the offspring indicated that he was the real father. Later matings using females known to be virgin confirmed the segregation. Burgess debated whether the black form might be a different species, and seemed to expect that if it were, the hybrid would have been intermediate; but today his results would be taken to mean that the red and black differed in one gene.

Later experimenters expected segregation, but in fitting their results to ordinary Mendelian rules were handicapped by difficulty of assuring virginity of the females. Most of the early supposedly hybrid progenies were obtained from pairs taken *in coitu* in nature, and under these circumstances the female might have mated earlier. Schröder,[29] recognizing this source of confusion in his crosses of *Adalia,* sought later[30] to remove it by using beetles just emerging from hibernation. After this precaution he got only one kind of offspring from each first cross; but even if spermatozoa could not survive over winter in the female, he could have got this expected result only if the phenotypically dominant parent were homozygous. The experiments of Johnson[16 17] on various species, and of Hawkes[8] on *Adalia* and[9] on *Coccinella* were often started with females not assuredly virgin, and some of the results were held to show they were not virgin—though heterozygosis might be the explanation of some such results. Forms regarded as belonging to different genera were taken in copulation by Marriner,[20 21] with progeny indicating segregation and some degree of dominance, though the interpretation was doubtful. The hybrid announced in the first of Marriner's papers was held by Capra[2] not to be a hybrid, merely the variety *10-pustulata* of *Adalia* (*Coccinella*) *10-punctata,* but the second publication was based partly on a known hybrid.

No hesitation in assigning Mendelian explanations to results of crosses was felt by Palmer.[24 25] She was able to cross, without difficulty, five forms regarded by many as distinct species of *Adalia.* Though no system of genes was proposed, she found segregation and varying degrees of dominance. Zimmermann[44] also arrived at simple Mendelian results in crosses between two varieties of *Epilachna chrysomelina,* in which light pronotum proved to be dominant over dark, and merged ocelli nearly dominant over separate.

Multiple Alleles

Some confusion in the early interpretations resulted from overlooking multiple alleles. In *Coelophora inaequalis* Timberlake[34] concluded that inheritance was segregative, but in some measure non-Mendelian because unexpected offspring appeared. His results were entirely regular, however, on the assumption of multiple alleles, as Dobzhansky[6] pointed out. The order of dominance in the triple series he studied is nine-spotted >normal >black. Tan and Li[33] proposed three pairs of genes to explain the patterns of *Harmonia axyridis,* but Hosino[12] concluded that the contrasted patterns are really multiple alleles. Tan

---

*Contribution from the Department of Zoology, University of Michigan.

and Li presented several results not in harmony with the multiple-allele explanation, but these Hosino[14] regarded as the results of experimental error—which can easily happen in work with these beetles. Hosino[13,14,15] added other alleles to this series, which now includes eight patterns. Between these alleles dominance is sometimes complete, sometimes partial or lacking.

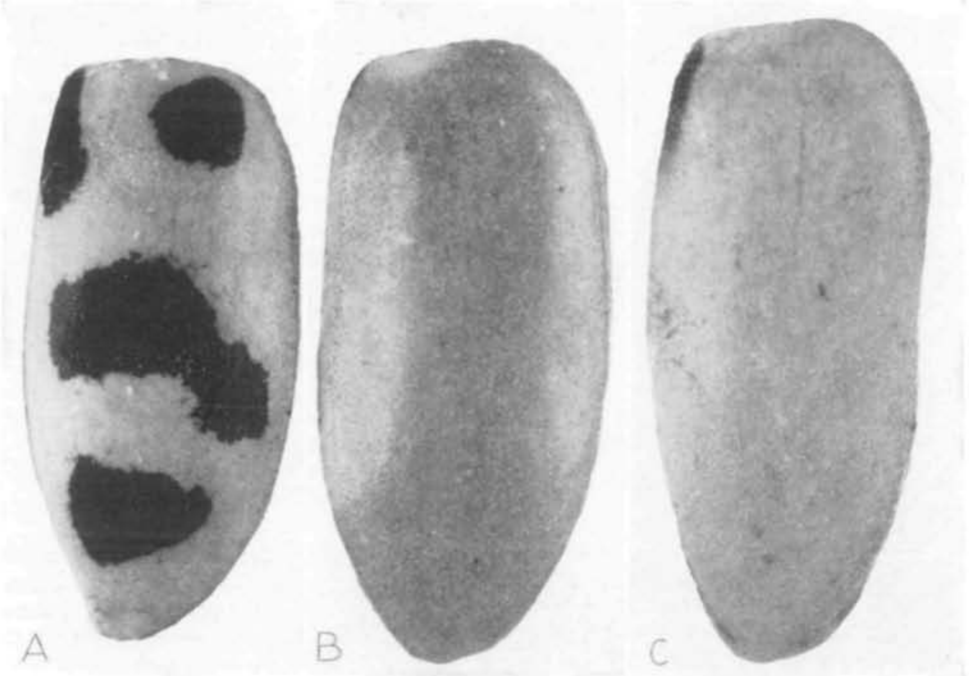
Palmer's results[24,25] are also explainable on the basis of a series of multiple alleles, which may have been her concept of their relations to one another though she does not specifically so state. The order of dominance (probably not always complete) in *Adalia,* as she found it, was apparently *melanopleura* >*bipunctata* >*annectans* >*coloradensis* >*humeralis.* There seems to be no specific reason in her work for putting *melanopleura* above *bipunctata* in this order, though she apparently assumes (Palmer,[25] p. 299) that that is its position. Support for the conclusion that these forms are multiple alleles is presumably afforded by the work of Lus[19] on the same species, *Adalia bipunctata.* Lus concluded that eight forms of this species are dependent on genes at the same locus, though the evidence is regarded by Timoféeff-Ressovsky[36] as not quite conclusive. The names given these forms are all different from those given to Palmer's "species," and from the illustrations presented most of them are phenotypically different from hers. With respect to two of them, however, there is no clear difference. Probably the form called by Palmer simply *bipunctata* (two black discal spots on a red ground on the elytra, and a black M on the pronotum) is the same as *forma typica* (gene S^t) of Lus; and Palmer's *humeralis* (red discal spots and red shoulder patches on black ground on the elytra, and a mostly black pronotum) could be identical with *4-maculata* (S^m) of Lus. If either of these suggested identities is real (and possibly even if they are not), the two series of alleles become a single one. If they do, however, the order of dominance is confused (perhaps by dominance-modifying genes); for *humeralis* is most recessive in the American alleles, *4-maculata* second most dominant in the Russian; and *bipunctata* is near the top of the dominance order in America, while *typica* is fifth in order in Russia. It would be interesting to know whether this large series may not also extend to another species, *A. decempunctata,* in which Lus discovered three alleles of a series. Among these three, the one at the bottom of the dominance order (*bimaculata*) is phenotypically very similar to the one (*sublunata*) at the top of the dominance order in *A. bipunctata.* One could speculate on the existence of a series of mutations of the same gene, spread through the two species, but divided into two groups by interspecific sterility. Lus does not indicate whether any species crosses were attempted.

Species crosses, it will be observed, are readily effected, though views of what constitutes a species (heretofore very discordant) may be profoundly influenced by the genetic work as the latter accumulates. Johnson[17] reported species crosses which were probably correctly so judged, since Johnson's tendency, according to Dobzhansky,[6] was to assemble species rather than split them. Even a generic cross (between *Adalia bipunctata* and *Coccinella variabilis,* see *ante*) was reported by Marriner[20] both as effected in the laboratory and as discovered in nature; and this hybrid was sufficiently fertile to be bred into later generations. The same author[21] suggests further that hybrids between *Adalia* and *Mysia* are found in England.

Indications of inheritance too vague to lead to any explanation were observed in *Harmonia axyridis* by Dobzhansky[4] before the conclusive genetic work of Tan and Li, and of Hosino. His discovery that each of several fluctuating (and overlapping) types had a different reaction norm suggested that these types had a genetic basis, and may well have been influential in bringing about the later experimental work. Correlations between different parts of the pattern could be interpreted on at least a physiological basis, perhaps a genetic one. Dobzhansky[4] established a correlation between pronotum and elytra in *Harmonia axyridis,* Schilder[27] between the parts of the elytral pattern in *Adonia variegata,* and Zarapkin[40] between the position of spots and their size and tendency to merge in *Propylaea 14-punctata.* These correlations, if not of genetic significance, must bear on questions of physiology of development, a field directly explored by Zarapkin[39] in *Coccinella 10-punctata* with respect to origin of pigment (which he regarded as being subject to a directed variability) and to formation of pattern. The fact that different races of *Epilachna* respond differently to temperature in the extent of their black spots (Timoféeff-Ressovsky[35]) presumably means that there is a genetic basis for this response. A number of other studies merely or chiefly described variability—for example, that of Reichert[26] for *Adalia bipunctata;* of Hosino[11] for *Harmonia axyridis;* of Meissner[22] for *Propylaea* and *Coccinella* with respect to the tendencies toward lightness and darkness; of Schilder[28] for *Propylaea* from which one could almost infer—as the author does not—dominance of reduced spotting over increased spotting; of Vogt and Zarapkin[38] for *Coccinella decempunctata* arriving at a statistical rule for the frequencies of patterns and at the conclusion that variation is directed; of Zarapkin[42, 43] on the relation between the frequency of spots and the time of their ontogenetic appearance, leading again to the concept of directed variability; of Schilder (in part, see *ante*) on *Adonia variegata;* and of Smirnov[31] and Timoféeff-Ressovsky and Zarapkin[37] in which lady beetles furnish part of the illustrative material for more or less purely mathematical considerations. While the phenomena described in these papers doubtless have a genetic basis in part, the authors are concerned with genetics only in a minor way or not at all. They may, however, have helped stimulate the directly genetic experiments.

One of the early uses of genetic knowledge of these beetles to the furtherance of biological theory will be (and has been) in relation to population statistics and geographic variation, and through these to the evolution of the coccinellid family. Dobzhansky[4] and Tan and Li[32] gave the proportions of the various types of *Harmonia axyridis* in different populations, while the frequency of omission of spots in *Hippodamia convergens* was ascertained by Dobzhansky.[6] Marriner[20] reported the seasonal prevalence of the red and black forms of *Adalia bipunctata* in England, the former being more abundant in spring, the latter in late summer. Additional varieties of this same species have been studied by Timoféeff-Ressovsky[36] near Berlin not only with respect to their frequencies in the population, but as to changes in those frequencies during the summer and as to their survival values in hibernation. The changes indicate that selection favors the black variety in summer (in agreement with Marriner for England), the red variety in winter. An increase in the frequency of many-spotted individuals of *Adalia bipunctata* in a certain area in England from one year to the next seems to have been brought about by Hawkes[10] by the artificial introduction of the darker forms into it. The tendency of the spots in *Coccinella 14-punctata* to merge with spots in front of or behind them, or beside them, was determined by Moderegger[23] for different populations, but the difference was not proven significant.

The importance of such statistics of populations is considerably enhanced if they are found to have a relation to geography, with or without any relation to climate. The lead in such geographic studies was taken by Dobzhansky[3] who traced the variation of two species of *Adalia* from Europe to central Asia, where they overlapped somewhat in their phenotypes, and Dobzhansky and Sivertzev-Dobzhansky[7] who, for *Coccinella septempunctata,* demonstrated a center for small spots in south central Asia and in Persia, and an increase in the spots radially from this area toward the west and northwest, and especially toward the east and northeast. A similar study of *Hippodamia convergens* (Dobzhansky[6]) showed that reduction of spots is much more frequent in California than in the



LADY BEETLE WING-COVER PATTERNS
Figure 4

A—Right elytron of the lady beetle *Hippodamia sinuata* var. *spuria*. *B* and *C* are right elytra of the spotless variety of *H. sinuata*. Note the short stripe on the inner angle of *C*.

eastern United States. Comparable geographic differences were observed for several other species, and Dobzhansky suspects a general relation to humidity and perhaps temperature in most of them. Such varieties, whether geographic or not, Dobzhansky[5] holds to have a genetic origin, in that they are differentiated out of an antecedent mixed population. Landis and Mason[18] also refer to geographic differences in variation in *Epilachna varivestris*, pointing out that in Mexico the tendency is to omit spots, in Ohio to merge them. Population differences in *Epilachna* were discovered by Zarapkin[41] with respect to the distribution of pigment among the several spots, such that specimens could be correctly allotted to their areas on that basis.

The literature of coccinellid genetics has been reviewed here in outline somewhat beyond the requirements of the new data to be presented in this paper, with the expectation that in any future publications in the same general field it will not be necessary to repeat the statement of fundamental relations.

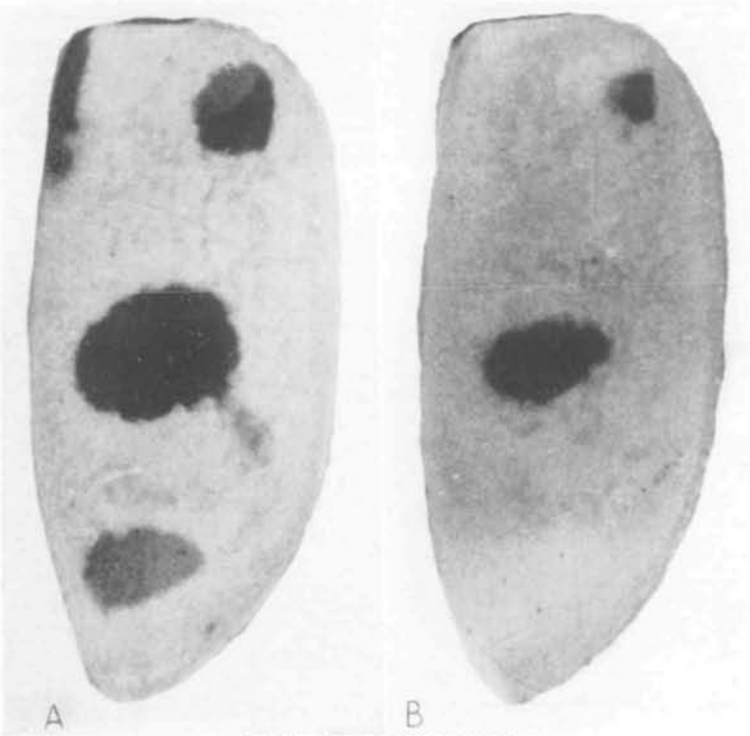
Pattern of *Hippodamia sinuata*

Through the courtesy of Professor H. B. Yocom I received in the spring of 1942 from near Eugene, Oregon, a mass of hibernating beetles most of which were *Hippodamia sinuata* var. *spuria*.*

The pattern of this variety is shown in Figure 4*A*. In the majority of individuals the spots are separate, except that across the middle of the elytron is a bilobed spot which, from a comparison with other species of *Hippodamia*, may be regarded as a merger of two spots. In many beetles, however, the bilobed spot is connected to a variable extent with the spot behind or in front of it, or

---

*Professor Melville H. Hatch kindly identified the material.



LACK OF DOMINANCE
Figure 5
Right elytra of two heterozygotes showing the lack of dominance of spotless and spotted. Of 20 hybrids between the spotted and the spotless form, one had no spots and the 19 others had much reduced spots.

with both of these. In none of the beetles in this hibernating mass was the bilobed spot connected with the scutellar spot which is shared by the two elytra at their inner front corners, though occasionally an angle projecting anteromesially from the bilobed spot suggests an approach to such a connection. The ground color is approximately ochraceous buff (Ridgway, Color Standards and Nomenclature).*

Among the spotted beetles were a few which had no black markings except (usually) a short and slender dark scutellar stripe (Figure 4*B*, *C*). Their color was essentially the buff of the ground color of the spotted type. This form is here called "spotless."

Beetles of both the spotted and spotless kinds were bred, and from their descendents were selected virgin females of the spotted form and males of the spotless, which were crossed. Of the 20 offspring obtained, one was entirely spotless (except the scutellar stripe which hereafter will be ignored), and the other 19 had much reduced spots. The size of the spots in these 19 varied considerably, but never even closely approached those of the spotted pattern. Two grades of the intermediate pattern are presented in Figure 5. The one at the left is not quite the darkest; it shows a slight indication of the outer lobe of the bilobed spot. In one other individual this outer lobe was a mere cloud, but separate from the inner lobe. At the other extreme of

---

*One beetle in the entire group, discovered too late to do any genetic work with it, had its spots so enlarged that the whole elytron was solid black except a narrow streak of buff along part of the margin.

SPOTTING PATTERNS
Figure 6

Types of coalescence of spots on elytra of *H. sinuata* var. *spuria*. Note that the bilobed central spot can be united by a bridge either to the forward spot (*A*), to the rear spot (*B*), or to both (*C*).

this series the spots became mere hazy patches. When only one spot was present it was at midlength; when two were present, it was usually the anterior outer (humeral) spot which accompanied the middle one.

The spotless pattern is thus not quite dominant over the spotted. There was overlapping of the heterozygote with the spotless homozygote, but always (in these experiments) a sharp gap between the heterozygote and the spotted homozygote.* To make the presentation of all the crosses uniform, the above results are included in the first line of Table I, where all the other successful experiments are recorded. All beetles with reduced spots, even if these are mere clouds, are listed as intermediate. The one spotless one in the first line is of course heterozygous, like the intermediates.

One mating not included in the table, spotless × spotless, was attempted several times, but offspring were obtained in only one experiment. In this successful mating one parent had faint cloudy spots, and was used on the chance that it might be homozygous spotless because spotless beetles were scarce at the time. The offspring were, however, of two kinds, spotless and intermediate. They are accordingly included in the second line of the table as progeny of intermediate × spotless.

With the exception of the seven beetles marked with an asterisk, the results in the entire table are in harmony with the assumption that only one gene differentiates spotless from spotted, and that

---

*In the classification of the hibernating mass there were only three or four beetles which required a second observation to decide whether they were intermediate or spotted.

dominance of spotless is incomplete. One of these seven (in the first line of the table) is known to be heterozygous; it is therefore justifiable to conclude that the spotless ones of the third and fourth lines are also heterozygous. Attempts to breed them for a more direct test failed.

Variations of spotted pattern

The only author to report the breeding of *spuria* is Johnson,[16] who regarded it as a separate species. He bred 13 females, sometimes after mating with unknown males, and records the pattern of their offspring. No later generations were reared. All these beetles were of the spotted pattern and the variations he observed were mostly related to the separation or coalescence of the spots. No very definite conclusions could be reached. He states that the inheritance of the scutellar stripe is segregative, but apparently this merely meant that it could be present or absent. He recognized two centers of variation of the spotting, but not two unit characters. The form which Johnson called *sinuata* he did not breed at all.

Whether the coalescence of the spots of the spotted pattern has a genetic foundation was not specifically tested in my own experiments, but some results bear on that question. All parents have been preserved, except a few which escaped or died and could not be found. Unfortunately, as a labor-saving device, the matings were not always of single pairs. Several females of one kind were confined with several males of a contrasted kind. When offspring were obtained, they could be the progeny of any one or more of each of the sexes among the adults. With respect to the characters which were being directly studied, and so long as the heredity proved to be simple, this method was satisfactory; but for any character which differed in some minor respect among the females or among the males, the results would be questionable.

In four of the matings between spotted and spotted all females and males used had the bilobed spot separate from the others. Their offspring included some with coalesced spots, the details being given in the first line of Table II. In other experiments one or more of the adults had the bilobed spot connected with either the humeral or with the apical (most posterior) spot (Figure 6). In Table II the experiments are described according to the type of coalescence shown by the possible parents and the progeny are sorted with respect to their coalescence. There is little in this table to suggest that the merging of spots is hereditary. More coalescence occurred in progenies which certainly were derived from parents without coalescent spots than in progenies whose parents may have had coalescent spots. It seems more likely that merging is dependent on developmental or possibly environmental fluctuations.

Frequency of the pattern genes

In their bearing on evolution, the importance of alternative genes depends on their abundance. While no comparison of the frequencies in different populations of the genes here studied can be made at once, the facts for this one population should be put on record. The beetles sent from Oregon were in a hibernating mass of over 23,000 individuals. It is found to consist of 20,974 spotted, 2,125 intermediate, and 143 spotless ones. The first of these numbers is fairly accurate, since there is little or no overlapping of the phenotypes of spotted and intermediate beetles. The other two numbers are doubtful because heterozygotes may have only the faintest indications of spots or be entirely spotless.

On the basis of these numbers it may be computed that 5.00% of the genes are S (spotless) and 95.00% s (spotted). It would be expected therefore that the spotted beetles (ss) would constitute 90.24% of the population, the intermediates (i.e., heterozygotes, Ss) 9.51%, and the spotless (SS) 0.25%. Thus the phenotypically spotless individuals, which constitute 0.62% of the total, are 2.46 times as abundant as the genotype SS should be. Only 40.7% of the phenotypically spotless beetles (about 58 of the 143) may be presumed to be genotypically *SS*. The other 85 spotless should be heterozygotes in which *S* is completely dominant. That is, in about 3.85% of the heterozygotes, spotless is completely dominant; in the rest the spotted gene comes to expression in some degree. These computations rest on the assumption of random mating and equal fertility and viability of all three types.

If the discrepancy between spotless pattern and the *SS* genotype represents merely the overlap of *Ss* and *SS*, the proportion of heterozygotes which were spotless was less in the natural population (3.85%) than in the experiments (15.22%). Another explanation of the discrepancy could be selective mating favoring that of spotless with spotless, though in the experiments such matings failed. The larger number of spotless can hardly be caused by differential mortality, for in the experiments the spotless beetles appeared to be the least vigorous. This appearance of lower vigor seems to be confirmed by the smaller number of spotless individuals among the progeny of intermediate × intermediate, in line 5 of Table I.

TABLE I. Results of crosses involving the spotted and spotless patterns of *Hippodamia sinuata*.

Parents		Offspring		
Female	Male	Spotted	Intermediate	Spotless
Spotted	Spotless	0	19	1 *
Intermediate	Spotless	0	11	12
Intermediate	Spotted	4	4	1 *
Spotted	Intermediate	24	16	5 *
Intermediate	Intermediate	90	114	41
Spotted †	Spotted	306	0	0

* These spotless beetles are interpreted as heterozygotes in which spotless is wholly dominant.

† Among these matings were some which used spotted beetles derived from intermediate parents, and which therefore could have borne the spotless gene had spotted been dominant.

TABLE II. Showing probable lack of inheritance of coalescence of spots in *Hippodamia sinuata*.

Possible Parents	Offspring			
	Bilobed spot distinct	Bilobed joined with humeral	Bilobed joined with apical	Bilobed joined with humeral and apical
Bilobed spot distinct	103	12	2	3
Bilobed joined with humeral in 3 of 11 parents	164	6	1	0
Bilobed joined with apical in 2 of 5 parents	9	0	2	0

Summary

The spotless pattern of *Hippodamia sinuata* differs from the spotted (variety *spuria*) in just one gene. The spotless type is not quite dominant; though a few of the heterozygotes are strictly spotless, most of them have reduced spotting. There is little or no overlapping of the phenotype of the heterozygote and that of the spotted homozygote. In an Oregon population, the spotless gene was present in 5% of the pertinent chromosomes, the spotted gene in 95%. Only about 41% of the phenotypically spotless beetles are homozygous for the spotless gene. The occasional fusion of spots, other than the pair in the middle of each elytron, in the spotted pattern has no clear genetic basis.

Literature Cited

1. Burgess, A. F. *U. S. D. A. Div. Ent. Bull.* 17:59-61. 1898.

2. Capra, Felice. *Boll. Soc. Ent. Ital.* 58: 113-116. 1926.

3. Dobzhansky, Th., *Russk. Entomolog. Obozr.* 18:201-212. 1924.

4. ——————. *Biol. Zent.* 44:401-421. 1924.

5. ——————. *Trans. 4th Internat. Congress Ent.*, Ithaca 2:536. 1929.

6. ——————. *Am. Nat.* 67:97-126. 1933.

7. Dobzhansky, Th., and N. P. Sivertzev-Dobzhansky. *Biol. Zent.* 47:556-569. 1927.

8. Hawkes, O. A. M. *Proc. Zool. Soc.* London. 1920:475-490. 1920.

9. ——————. *Ent. Month. Mag.* 63:203-208. 1927.

10. ——————. *Ent. Month. Mag.* 63:262-266. 1927.

11. Hosino, Y. *Dobutsugaki Zasshi* 45: 255-267. 1933.

12. ——————. *Jap. Jour. Genet.* 12: 307-320. 1936.

13. ——————. *Jap. Jour. Genet.* 15: 128-138. 1939.

14. ——————. *Jour. Genet.* 40:215-228. 1940.

15. ——————. *Jap. Jour. Genet.* 16: 155-163. 1940.

16. Johnson, R. H. *Carneg. Inst. Wash. Pub.* 122:1-104. 1910.

17. ——————. *Proc. 7th Int. Zool. Cong.* Cambridge, Mass. 1907:409-410. 1912.

18. Landis, B. J., and H. C. Mason. *Ent. News* 49:181-184. 1938.

19. Lus, J. *Bull. Bureau of Genetics*, Leningrad 6:89-163. 1928.

20. Marriner, T. F. *Ent. Rec. and Jour. Var.* 38:81-83. 1926.

21. ———————. *Ent. Rec. and Jour. Var.* 40:176-177. 1929.

22. Meissner, O. *Ent. Zeitschr.* [Frankfurt a. M.] 43:55-57, 81-83, 126-127. 1929.

23. Moderegger, Ursula. *Zeit. wiss. Biol. Abt. A. Zeit. Morph. u. Oekol. Tiere* 26:327-333. 1933.

24. Palmer, M. A. *Ann. Ent. Soc. Am.* 4:283-308. 1911.

25. ———————. *Ann. Ent. Soc. Am.* 10:289-302. 1917.

26. Reichert, A. *Ent. Jahrb.* 1904:179-181. 1904.

27. Schilder, F. A. *Ent. Blätter* 24:129-142. 1928.

28. ———————. *Ent. Zeitschr.* [Frankfurt a. M.] 42:188-189, 199-200. 1928. 249-253. 1929.

29. Schröder, C. *Allg. Zeit. Entomologie* 6:355-360, 371-377, 7:5-12, 37-43, 65-72. 1901, 1902.

30. ———————. *Zeit. wiss. Insektenbiol.* Berlin. 5:132-134. 1909.

31. Smirnov, E. *Verh. 5. Internat. Kongr. Vererbungswissenschaft,* Berlin, 1927. Leipzig. Borntraeger. 5:1373-1392. 1928.

32. Tan, C. C., and J. C. Li. *Peking Nat. Hist. Bull.* 7:175-193. 2 pl. 1932-33.

33. ———————————. *Am. Nat.* 68: 252-265. 1934.

34. Timberlake, P. H. *Proc. Hawaiian Entom. Soc.* 5:121-133. 1922.

35. Timoféeff-Ressovsky, H. *Proc. Sixth Internat. Cong. Genetics.* 2:199-200. 1932.

36. Timoféeff-Ressovsky, N. W. *Biol. Zent.* 60:130-137. 1940.

37. Timoféeff-Ressovsky, N. W., and S. R. Zarapkin. *Biol. Zent.* 52:138-147. 1932.

38. Vogt, O., and S. R. Zarapkin. *Jour. Psychol. u. Neurol.* Berlin. 39:447-454. 1929.

39. Zarapkin, S. R. *Zeit. wiss. Biol. Abt. A. Zeit. Morph. u. Oekol. Tiere* 17:719-736. 1930.

40. ———————. *Zeit. wiss. Biol. Abt. A. Zeit. Morph. u. Oekol. Tiere* 18:726-759. 1930.

41. ———————. *Zeit. wiss. Biol. Abt. A. Zeit. Morph. u. Oekol. Tiere* 27:476-487. 1933.

42. ———————. *Zeit. wiss. Biol. Abt. A. Zeit. Morph. u. Oekol. Tiere* 34:565-572. 1938.

43. ———————. *Zeit. wiss. Biol. Abt. A. Zeit. Morph. u. Oekol. Tiere* 34:573-583. 1938.

44. Zimmermann, K. *Zeit. induk. Abst. Vererb.* 71:527-537. 1936.

◆

THE SCULPTURING OF GROWTH

ALTHOUGH not published as a continuation of the author's well known *Chemical Embryology,* the present work* closely resembles it in format and method of approach. As in *Chemical Embryology,* the attack is on a large scale over a wide front, with the difference that in this book the main effort is concentrated on the organizer problem. *Biochemistry and Morphogenesis* is divided into three parts respectively titled: The Morphogenetic Substratum, The Morphogenetic Stimuli, and The Morphogenetic Mechanisms. Part I, consisting of 93 pages, summarizes recent literature dealing with the chemical composition of the egg and with problems of embryonic nutrition. It brings up to date the corresponding chapters of *Chemical Embryology.* Part II, 405 pages, presents an exhaustive summary of published experiments bearing on the physiology of determination in vertebrates and invertebrates. Part III, of 172 pages, covers recent work on the special metabolism of the embryo. There follows a glossary of special terms and an astonishing bibliography of approximately 5,000 references, listing apparently every publication of any importance which has appeared in this field in the last ten years. The volume is fully indexed. Possibly as a compromise with paper-rationing, the author has adopted an unfortunate shorthand for indicating chemical structures; otherwise there are but few signs of war in the make-up of this book. It is noteworthy indeed that a scientific treatise of such size and elaborateness has been published in England at this time.

The Evocator Mystery

The most important section is Part II which occupies over half the book, and deals with the complicated field of organizer phenomena wherein embryologists caught the first exciting glimpses of a possible causal connection between

---

***Biochemistry and Morphogenesis,* by Joseph Needham; xvi + 787; 328 figs.; $12.50; Macmillan, 1942.