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Color and Color-Pattern Mechanism of  
Tiger Beetles

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**COLOR AND  
COLOR-PATTERN MECHANISM  
OF TIGER BEETLES**

WITH TWENTY-NINE BLACK AND  
THREE COLORED PLATES

BY

VICTOR E. SHELFORD

Contributions from the  
Zoological Laboratory of the University of Illinois, No. 93

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## INTRODUCTION

In the analysis of characters made the basis of studies of variation, orthogenetic trends, experimental modification and heredity, noteworthy advantages are associated with the study of large groups of species in which divergence and modification have proceeded in various directions. The material should be plastic so that the laws governing response in characters can be determined. The ontogeny of the characters should be of such a character as to show the general ground plan of the system and its relation to the existing adult characters and their variations. It is further desirable to be able to breed the organism, segregate pure lines, and cross various species. There is a strong tendency of late years to regard the breeding and the breeding results as superior to the other attempts at character analysis. This has proceeded to such an extent without adequate physiological analysis that one writer (Riddle, 1909) designated the method of cross breeding "the mixing of unknowns". The primary object of this paper is to show the nature of the color and color-pattern mechanism of the elytron.

In the matter of qualifications of material the tiger beetles are admirably adapted to all the needs enumerated above, but since one year at least and normally two are necessary for a generation, only a few single generations have been bred. For this reason the idea of breeding them was abandoned. It is also a purpose of this paper to show that breeding is not the only method by which adequate analysis can be reached, i.e., unless the laws governing heredity are a system entirely a part from those governing the modification of parts during ontogeny and the normal course of variation, which seems to be the tacit assumption of various students of heredity in the not too distant past.

I shall indicate further that orthogenetic tendencies, if directive tendencies are to be so named, are numerous and in a large series of species present a confusing set of groups which are excessively complicated and reduced to any simple system, as claimed by Eimer and von Linden for Lepidoptera or for a limited number of species by Whitman, with difficulty. Still, large tendencies with numerous minor ones within them may be detected. It will be shown that the laws governing the modification of patterns apply alike to general, probably hereditary tendencies and detailed response under experimental con-

ditions. It will be shown that biogenetic law must be applied with caution and is not of such broad application as is held in some quarters, being inapplicable to various characters altogether.

The brilliant colors of the group are due to physical phenomena determined by Professor Michelson, and leave no place for the biogenetic law in connection with the development of color during ontogeny. It will be shown further that color is closely correlated with general physiological condition and is modifiable by conditions which affect general metabolism. The results here presented are based on several years of observation.

In 1903 the writer undertook a study of variation of the tiger beetles. The work here presented is the outgrowth of this beginning, and indeed includes some small portions regarding color patterns that were written in that year. The work has been prolonged for many reasons, but chief of these was the very large number of species in the group and the fact that an adequate understanding of the material could not be attained without consulting many large collections. Further, the experimental results obtained in 1906 demanded a first-hand study of the variations of the species concerned and their natural habitats. The accumulation of material and data was not completed until 1911. Some of this had to be studied, drawings made, etc., which with numerous other duties and enterprises under way made necessary much time to put it into the present form.

A family with upwards of 1300 species of which more than 600 are in one genus and with characters which can be studied and analyzed, appeared to afford material which was sufficiently promising to justify delay. In the fourteen years that have elapsed since the problem was first undertaken at the suggestion of Dr. C. B. Davenport, the attention of biologists has shifted from variation, which was then the chief topic of interest, to experimental modification of characters, and finally to the methods of modern genetics. Various men have made numerous suggestions regarding the work, but in its final preparation the writer has been able to use only a few of them in a general way, and an attempt is made to present the facts and conclusions growing out of the material as simply as possible.

#### MATERIALS AND METHODS

The material which has been used as the basis of this work has consisted of collections in the family Cicindelidae of the world, extensive collections of several North American species, repeated year-to-year collections of a few species in Illinois and Indiana, series of observations on the ontogeny of color in a small number of North American species,

and experimental modification of a number of species which has assisted in the analysis of the color patterns.

The collections studied have covered most of the species of the family, which is divided into several tribes by W. Horn in the *Genera Insectorum* (1915). The subfamilies herein named were in part given as families in the *Systematischer Index* of the same author (1906), in which he presented a preliminary list of the species which he later published in the *Genera Insectorum*. Accordingly, in my previous papers on the subject (1906, 1908, 1912, 1914, 1915) the "Index" was followed almost entirely in the matter of nomenclature and order of arrangement.

The groups represented in the family as outlined in *Genera Insectorum* are as follows:

Subfamily	Number of species
Subfamily Ctenostomini (tree dwellers)	
Pogonostoma; Madagascar.....	32
Ctenostoma; tropical America.....	45
Subfamily Collyrini (nearly all tree dwellers)	
Tricondyla; India.....	27
Collyris; Oriental region.....	104
Subfamily Mantichorini (ground dwellers)	
Mantica; Africa.....	1
Mantichora; Africa.....	5
Subfamily Megacephalini (ground dwellers)	
Platyechila; South Africa.....	1
Pynoehila; South America.....	1
Amblychila; Western U. S. A.....	2
Omus; Western U. S. A.....	4
Aniaria; Northeastern South America.....	1
Megacephala; southern U. S. to Argentine, Africa, Arabia, Persia, Australia.....	68
Oxyechila; middle America.....	25
Pseudoxyechila; Andes, Costa Rica to Bolivia.....	1
Chiloxia; Andes of Ecuador to Bolivia.....	1
Eueallia; Andes of Ecuador and Columbia.....	1
Subfamily Cicindelini; ground dwellers	
Dromica; southern half of Africa.....	82
Prothyma; Africa, Madagascar, Asia, and the Malay Archipelago.....	50
Dilatotarsa; Malay Archipelago.....	1
Caledonomorpha; New Guinea.....	1
Distipsidera; Australia and New Guinea.....	8
Caledonica; New Guinea.....	9



Nickerlea; Australia.....	2
Rhysopleura; Australia.....	1
Euprosopus; Brazil.....	2
Langea; Peru.....	1
Iresia; continental tropical America.....	8
Therates; Malay Archipelago.....	33
Odontochila; South America, Malay Pen. and Islands .....	75
Prepusa; South America).....	3
Oxygonia; South America.....	15
Opisthencentrus; Brazil.....	1
Cicindela; world-wide distribution .....	686
Eurymorpha; Africa.....	1
Apteroessa; India.....	1
	<hr/>
	1299

The group contains some 35 genera and upwards of 1300 species and subspecies. In the figures above the subspecies of *Cicindela* numbered in Roman in Horn's *Genera Insectorum* list, which number 55, are included, but subspecies numbering more than 8 in *Megacephala* alone, and several in other genera, are not included.

There are very few of these 1300 races which the writer has not seen in some one of the particularly numerous and complete collections studied. Those studied quite completely are: British Museum of Natural History; Hope Collection, Oxford University; Cambridge University; Private Collection of Mr. Basil G. Nevinson, London; Private Collection of Dr. Walther Horn, Berlin; Zoologisches Museum, Berlin; Private Collection of Doctor Gestro, Genoa; Jardin des Plantes, Paris; Museum of Comparative Zoology, Cambridge, Massachusetts; United States National Museum; Philadelphia Academy of Science; American Museum of Natural History, New York; and the University of Chicago collection including an old collection once the property of John Akhurst, Brooklyn, several purchases from Hermann Rolle of Berlin, and the material secured by exchange for other species in the Akhurst collection, and material purchased and collected for the writer by the University, and specimens collected on the excursions supported by the University. In addition to this the writer secured a collection of exotic material from Mr. John D. Sherman in exchange for *Dytiscidae* and numerous specimens by exchange and gift from numerous American and foreign collectors. Of the few species not seen several are represented in figures which show the color patterns.

Many of the drawings presented are from the collections in question and are appropriately designated in the groups of figures in the

succeeding pages. The meaning of the designations is as follows: B, British Museum; C, Cambridge University; D, Berlin; G, Gestro; H, W. Horn, Berlin; M, U. S. National Museum; N, Nevinson; O, Oxford University; P, Paris; S, Shelford; U, University of Chicago.

While none of the patterns of the genera other than *Cicindela* are of a type differing from the general plan of the *Cicindela*, patterns are very often wanting or very simple, such as the simple cross bands in *Collyris*. In course of the examination of the several collections named, a great abundance of variation has been noted in some of the commoner representatives of the groups, not only of *Cicindela* but others also.

The taxonomic arrangement of *Cicindela* by Doctor Horn in the *Genera Insectorum* is especially fortunate. He has arranged the species into a number of groups on the basis of the distribution of hairs on the head, thorax, abdomen, tarsi, labrum, and of other structural characters, but without reference to color patterns. He gives 174 groups apparently not duplicated in the different regions and 16 represented in more than one zoogeographic region by the same or closely related species. These 174 groups are distributed as follows: Ethiopian region, 34; Oriental region, 48; Australian region, 22; Palearctic region which he extends to include China, 20; Nearctic region, 24; Neotropical region, 26. The groups found in more than one region and which are counted in the one with most species, are as follows:

TABLE I

Showing the Number of Species in Regions by Groups as Designated by a Common Species

	Ethiopian	Oriental	Australian	Pale- arctic	Nearctic	Neo- tropical
<i>singularis</i> Chd.....	1	2	.....	5	.....	.....
<i>melancholica</i> Fab.....	21	7	.....	5	.....	.....
<i>donegalensis</i> Chd. ....	4	2	.....	6	.....	.....
<i>nilotica</i> Dj. ....	1	1	.....	.....	.....	.....
<i>germanica</i> L. ....	70	.....	.....	4	.....	.....
<i>foveolata</i> Schm. ....	.....	1	1	.....	.....	.....
<i>laetescripta</i> Mtsch.....	.....	1	.....	1	.....	.....
<i>10 guttata</i> Fab. ....	.....	3	1	.....	.....	.....
<i>striolata</i> Illig. ....	.....	2	1	.....	.....	.....
<i>discreta</i> Schm. ....	.....	2	1	.....	.....	.....
<i>semicineta</i> Br. ....	.....	1	3	.....	.....	.....
<i>brevisponosus</i> W. Horn	.....	3	.....	1	.....	.....
<i>carthagena</i> Dej. ....	.....	.....	.....	.....	16	6
<i>argentata</i> Fabr. ....	.....	.....	.....	.....	6	8
<i>trifasciata</i> Fabr. ....	.....	.....	.....	.....	1	3
<i>macrocnema</i> Chd. ....	.....	.....	.....	.....	3	2

In the above list species occurring in two are counted in both. So far as practicable these pilosity groups have been considered in working up, arranging, and discussing the patterns.

Considerable change has been made in the nomenclature and arrangement of species in the Genera Insectorum as compared with Doctor Horn's Index. The paper had progressed so far with the Index as a basis that it was thought not to be practicable to change it to agree with the newer work.

The extensive collection of North American species belong to the first group in Horn's series for the Nearctic region. This group includes *tranquebarica* and will be referred to as the *Tranquebarica* Group. These are characterized as follows: The four anterior trochanters have fixed hairs, cheeks naked, or with isolated hairs, clipeus often hairy. Frons with discoidal or supraorbital hairs; median portion of the frons never proportionately supplied with more or less short, close lying, downward directed hairs; frons never hairy above the antennal insertion. The disc of the middle frons is often hollowed out or sharply separated from the fore frons by its steepness. The first antennal segment is often thickly covered with outstanding hairs. The pronotum has at least rudimentary hairs, often circumdiscally and discally hairy; hairs often long and fine and never decumbent except when very numerous; free anterior and posterior border of the pronotum not hairy. The prosternum is always naked. The lateral portion of the breast is always thickly covered with hairs. The hind border of the femur and sometimes the foreborder also covered with fine short decumbent hairs; hook-formed hairs never present; hairs on the hip and superorbital border most numerous. This group stands in close relation to the European group to which *campestris* belongs. The main group includes *formosa*,\* *venusta*, *limbata*, *purpurea*,\* *ancosisconensis*, *duodecemguttata*,\* *hirticollis*,\* *latesignata*, *tranquebarica*,\* *tenuicincta*, *bellissima*, *longulabris*, *eureka*, *oregona*, *senilis*, *willistoni*, *fulgida*, *pulchra*, *pimeriana*, *scutellaris*.\* In addition to this, collections were made of *C. sexguttata* which stands in a group by itself. Those starred were studied especially. Collections of these species representing complete catches were supplied by C. S. Brimley, E. G. Smyth, C. A. Frost, L. H. Joutel, Rev. J. C. Warren, and Dr. C. F. Adams. Collections were made by the writer in various parts of the United States.

The species about Chicago, especially *scutellaris*, were collected through the year from the same locality with a view to getting the seasonal variation of the species and any variation from generation to generation.

The color ontogeny work was done on material dug in the larval stage at Glencoe, Illinois (*C. limbalis*); at Gary, Indiana, (*C. tranquebarica*); at Miller, Indiana (*C. lecontei*); at Lyons, Illinois (*C. purpurea*); at East Chicago, Indiana (*C. repanda*); Chicago vacant lots (*C. punctulata*); and Suman, Indiana (*C. sexguttata*). These larvae were reared in a greenhouse in which the temperature was about 4 to 8 degrees C. higher than the out-door soil temperature. This accelerated the appearance only a little and did not show modification of color or pattern. The larvae were reared in sand, either in cylindrical lamp chimneys, setting in screen bottomed boxes or in screen bottomed boxes. When the majority of larvae had pupated all were removed to small square watch glasses, lined with filter paper and moistened with 2%  $H_2O_2$ . These were piled up so as to cover each other and kept in a cool room, and watched closely to secure as many as practicable at the time of emergence. The elytral material was nearly all killed in a pero-sulfuric acid killing fluid and cleared and mounted in balsam, but some was preserved in glycerine jelly direct with good results. They were preserved at different intervals after emergence.

The material for experiments was collected from the same places as that for ontogeny study and was subjected to high and low temperatures in an apparatus to be described later.

The writer is indebted to Dr. C. B. Davenport, the late Professor C. O. Whitman, Professor C. M. Child, and Professor W. L. Tower for suggestions during the first four years of the work (1903-1907). He is further indebted to the University of Chicago for funds amounting to \$400 and to Professor and Mrs. F. R. Lillie for funds amounting to \$200 to cover expenses connected with the study and collection of the group. The Graduate School and Department of Zoology of the University of Illinois provided for later stages of the work.

Acknowledgments are due Miss Annette Covington for making the water color drawings of the ontogenetic stages and the other changes in color during the life history. Mr. K. Toda made the drawings of the geographic races shown in color and also the stippled drawings of ontogeny.

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R. Shelford, Hope Collections, Oxford; Professor David Sharpe, Cambridge; Professor Kolbe, Berlin; Mr. P. Lesne, Paris.

The following permitted me to study their private collections with a considerable loss of time and attention: Dr. Walther Horn, Berlin; Mr. Basil G. Nevinson, 3 Tedworth Square, London; Mr. Gestro, Genoa.

A considerable number of men whose names appear below gave me data on the distribution of the species in their collections, loaned or presented specimens, or did similar service through making extensive collections which were exchanged. For this I am debtor to Messrs. C. F. Adams, C. N. Ainslie, Geo. G. Ainslie, E. M. Anderson, A. W. Andrews, Germain Beaulieu, Biederman, Wm. Beutenmuller, Albert L. Barrows, C. S. Brimley, T. C. Brues, T. D. A. Cockerell, I. W. Cockle, Norman Criddle, F. F. Crevecoeur, C. C. Deam, G. M. Dodge, Edwin H. Edwards, J. D. Evans, S. A. Forbes, E. P. Felt, E. D. Harris, R. V. Harvey, G. W. Herrick, H. R. Hill, J. S. Hine, A. D. Hopkins, W. Horn, James Hunsen, S. A. Johnson, James Johnson, W. Knaus, Chas. W. Leng, H. P. Loding, D. E. Lantz, W. MacIntosh, G. P. Mackenzie, L. E. Marmont, A. L. Melander, F. W. Nunenmacher, W. E. Rumsey, L. E. Ricksecker, A. G. Ruthven, Franklin Sherman, H. F. Snow, E. G. Smyth, Tom Spalding, Chas. Stevenson, T. B. Symons, H. B. Walden, H. F. Wickham, T. N. Willing, R. S. Woglum, R. H. Wolcott, E. O. Wooton, E. C. VanDyke, E. P. Venables, S. S. Visser.

## ANALYSIS OF COLOR PATTERNS

## COLOR PATTERNS AND ELYTRAL STRUCTURES

In the Cicindelidae usually only, the elytra have color patterns. These are merely sack like outgrowths supplied with nerves, trachea, and blood spaces. The cuticular covering is in two layers; the outer portion is a hard and relatively homogeneous layer known as the *primary cuticula* and on the upper side is usually characterized by the presence of saucer-shaped depressions, somewhat hexagonal in form, fitting together with common rims. These rims usually correspond to the positions of the points of contact of the hypodermal cells and accordingly each cup corresponds to a cell (Packard, 1900 text). Some forms in the family, e. g., the *Tetrachas* and the *Amblychila* do not have these cups; the surface is smooth. In certain areas the primary cuticula is pigmented and in certain areas clear and transparent. This gives the color pattern. Some species are almost entirely pigmented; some entirely without pigment. Beneath the primary cuticle is the secondary cuticula which is laid down in successive layers during the life of the individual and in the forms like *Amblychila cylindriformis*, and *Phaeoxantha klugi* is essentially uniform in character. It contains some spaces, probably pore canals, which are empty of cell contents except for the layer in actual contact with the cells. A few of these pore canals can be detected in the secondary cuticula of *Tetracha carolina*. In *Cicindela* the secondary cuticula beneath the pigmented areas of the elytron is clear and transparent and entirely free from the "pore canals" and interlamellar spaces, while beneath the unpigmented areas it is full of the "pore canals" and large interlamellar spaces, and these having been left empty by the retreat of the cells from the successive layers; they give the effect of a white or straw color depending upon the color of the secondary cuticula itself. In these regions, beneath the unpigmented primary cuticula, it is about twice as thick as beneath the pigmented parts (Fig. 1, Pl. I). The color pattern may accordingly be described in terms of pigment and lack of pigment, the so-called markings being without pigment.

The two walls of the sac-like elytron are held together by chitinous pillars or columns which in the adult appear in cleared elytra. The different layers of cuticula show here as rings around the original

central spindle (Shelford 1915:243, Fig. 1). In the Cicindelidae the chitinous columns are not arranged in any very definite manner but in some cases they retain their pigment within areas that are not otherwise pigmented.

Hairs which in a primitive insect usually cover the wing entirely are present in nearly all tiger beetle elytra. In the *Mantichoras*, observed representative of the Pogonostomidae, and one of the Megacephalidae, *Megacephala (Tetracha) aequinoctialis*, the elytra are more or less completely and uniformly covered with small hairs. Under the microscope the hairs may be located on the pigmented area of the elytra by the light area which is produced by the thin cuticula at the base of each hair. Hairs appear on the whole to be less common in the unpigmented areas and when present usually are surrounded by a narrow rim of pigmented cuticula. Hairs occur in practically all groups, though they have been lost from the majority except for a few at the base of the elytron and scattered along the tracheae (Shelford, 1915:243, Figs. 1 to 3). These are present in *Cicindela* and are shown by small circles in figures 2 to 29, plate I to III.

The elytra of many species are marked with pits. Close examination under the microscope with both transmitted and reflected light shows that, in the majority of cases, the pits are over the center of the chitinous columns and bear no relation to rudimentary hairs as Dr. W. Horn has suggested. I have seen no pits that would appear to represent rudimentary hairs though they may occur.

There are sometimes thickenings running lengthwise of the elytron as in *Dominica* (Shelford, 1915: Figs. 35 and 36). While these thickenings run parallel with the trachea, they are usually between rather than coincident with them, except in *Caledonia* (Fig. 25). There are, however, some thickenings on the under side of the elytra of most species which correspond in a general way to veins (particularly in *Mantichora*). The outer and inner margins of the elytra are always thickened and resemble veins, almost invariably containing tracheae. The subcosta usually follows the costa very closely at the base of the elytron but just behind the middle it turns inward away from the margin in a vein like thickening. The radius is in a distinct thickening of the elytron which proceeds from the base for a short distance. This is very constantly present. Aside from this nothing comparable to veins is present but the rows of chitinous columns are often so arranged so as to give distinct and direct spaces running the length of wing. These are occupied by the principal tracheae. In some cases the spaces appear very clearly on the under side of the elytron and in *Mantichora* there are distinct ridges over them which have every appearance of veins.

The elytral tracheation of the *Cicindela* has been observed by the writer in about one hundred species. The elytra of the newly emerged emagoes of ten North American species have been studied in some detail. Nearly all the common North American species and about fifty exotic species have been studied in less detail by mounting dried elytra in hot Canada balsam containing little or none of the usual solvents. The main tracheal trunks and some of the branches remain clearly visible in such mounts for several hours.

In terms of the system of classification proposed by Comstock and Needham, the usual tracheae present (Figs. 18 and 21, Pl. II) are the costa (*Co*) which branches near its distal end, and subcosta (*S*) which lies close to the costa on the outer edge of elytron; the radius (*R*) and media (*M*) which lie in the medium portion of the elytron; the cubitus (*Cu*) which lies along the suture, and (*A*) the anal rudiment which lies next to the scutellum.

The six trunks common in insects are represented in but two genera (*Amblychila* and *Mantichora*), which have rudimentary wings and specialized elytra fastened together in the adult (Shelford, 1915). These trachea are demonstrated in the adult dried elytra without any difficulty. In *Omus*, which is closely related to *Amblychila*, the radius and media have disappeared except for rudiments. The cubitus is the principal trachea. With the exception of *Omus* and *Amblychila* it is the anal that has degenerated farthest. *Collyris* was never very satisfactory for study, but it appears that the cubitus is reduced and the anal wanting. In *Platychila pallida* (Shelford, 1911: Fig. 7) the commonest type of tracheation of the family and probably among the most generalized, so far as the first four trachea are concerned, is shown. The anal is much reduced.

The number of small branches and cross connections is large and too variable to be correlated with other specific characters or with color-pattern characters. Figures already published (Shelford, 1915: Figs. 10 to 19) illustrate this fact. The two elytra of an individual show a marked difference. It is evident then that only the main trunks are at all constant. The costal branch at the center the posterior third of the elytron at the beginning of the curve is very characteristic of *Cicindela* but bears an important relation to color pattern only in some cases.

Figures 2 to 33, plates I to III are selected to show the relation of unpigmented areas to the main tracheal trunks. Figure 2 shows four cross bands which are cut across by the tracheae. Figures 3 and 4 show the same type of pattern but with the cross bands narrower, the middle one broken in the region of the trachea toward the right and with a suggestion of two or three stripes. Figure 5 shows a similar condition but



with the spots in the upper right-hand third of the elytron missing. Figure 6 shows a suggestion of seven cross bands as numbered. Figures 8 and 9 are similar but somewhat broken and with some tendency to forming longitudinal stripes between the tracheae. Figure 9, Plate I shows a longitudinal row of spots and figures 10 to 13, Plate II either rows of spots or continuous longitudinal bands between the tracheae. Figures 14 to 21, Plate III show forms that have lost most of their pigment and have retained it only in the lines of the tracheae. Figure 18 shows a form that appears to have double longitudinal lines between the tracheae and has lost the unpigmented areas in the anterior part of the elytron. Figures 16, 20, and 21 show forms that are highly specialized as to the patterns and have lost most of the pigment and the *media* trachea is almost gone. It will be noted that there are many interesting curves and branches that are related to the color pattern.

Figures 23 to 25, plate III show an oblique joining of the markings to form a vitta that is not related to the trachea and is rather rare, constituting an exception to the usual rule.

As a result of this study of the figures it is seen that in the color patterns of the genus *Cicindela* exists a system of markings that is related to the tracheae, and also is arranged with reference to the cross bands of which there are five, two of which may be divided as to make seven and that these are arranged as follows: There is a cross band in the center of the longest measurement of the elytron. This location is shown to be the same in essentially all of the cases by actual measurement. There is one at the tip and one at the base, with one or two arranged respectively between each of the latter and the middle one. These intermediate bands are most commonly represented as *one* but are some times divided, but in any case its center, or the center of the intervening pigmented area is half-way between the two adjacent, unpigmented more permanent cross bands. It is also evident that there is a possibility of fusion of joining of light areas, so that these lines of fusion are in the spaces between the tracheae and in the region of the cross bands.

The areas near the hairs described in a preceding section are the very last to lose their pigment in the forms that become almost entirely without pigment. It is to be noted that in the forms that have the longitudinal stripes and cross bands broken up, the *media* is almost entirely gone. It has been shown that these cross bands are the most constant wing markings in insects and are usually represented as the *five* first mentioned. I have gone over very large series of Coleoptera, (Tower, 1906), and find that this is true for this order, while cross bands in the Lepidoptera (Braun, et al. cited), Diptera, Orthoptera, Tricoptera, Plecoptera, Hemiptera, have been discussed by Von Linden,

Eimer, et al. In the Lepidoptera (Mayer), however, the line of the veins is the one in which pigment is longest absent, but in the Diptera both living and fossil there is a uniformly denser pigmentation of the veins. Doctor Williston tells me that it is true of the fossil forms, and Doctor C. F. Adams found in the development of the color pattern of some common flies that pigment first appeared along the cross veins and spread from these. In the Hymenoptera the veins are often pigmented and the same is true of the Mecoptera, Plecoptera, some Homoptera, etc. Pigment is usually found in muscle attachments and wherever rigidity is necessary; this has been reported by Tower (1906) in Coleoptera, and in *Polistes* by Enteman (1905). Since the veins are supporting structures, one would expect that they would usually be pigmented. The great development of the secondary cuticula in the Coleoptera might since the elytra are no longer used as wings, show modification characterized by the loss of this character in some cases. I find no observations on the secondary cuticula of the wings of Lepidoptera.

In the Ctenostomidae are found bands in some of all of these positions noted in *Cicindela* (Figs. 26 and 27, Pl. III, also 376, Pl. XVI.)

In the Collyridae it appears that the band at the base of the elytron (1), one in the middle (4), and the one at the tip (7), are quite common and well developed (one or all). *Collyris celebensis* Chd. (Fig. 28) and *arnoldi* McL., *horsfieldi* McL., *fasciata* Chd. et al. have such bands. In Theratidae are found markings which conform to the cross bands of *Cicindela*, (Figs. 332 to 337, Pl. XVI), but the areas represented in the two ends of the elytron may be much extended (Figs. 236 and 237, Pl. XIII).

Turning to the other form of the Cicindelidae proper, one finds that in the Euryodini and the Odontochilini markings occur in the same relations to structures as those already described. Among the Euryodini, in Caledonia occur some of these cross bands indicated, and in addition a very interesting thickening of the elytron in the lines of the tracheae (Shelford 1915: Fig. 25). These may or may not correspond to the thickenings that are associated with the veins of other insects, for in the Dromicini, (Cicindelidae proper) we find thickenings that lie between the veins and may be regularly arranged (l. e. Figs. 35 and 36). It will be noted that there are spots in places corresponding to those already mentioned for example, crossbands in figure 29 representing the Odontochilini, and longitudinal stripes in figure 30 representing the Dromicini.

In the Megacephalidae the color patterns are in some cases like that

shown in figures 370-372, plate XVI, which accord with those of Cicindela. In *Megacephala klugi* we find a curious dark spot in the position of the cross veins between the subcosta and the ramus which corresponds to the condition that Tower (1906) has called attention to in the Coleoptera, Lepidoptera, etc., but it is not of frequent enough occurrence to be significant. I know of no color patterns in the Palaeomantichoridae or the Neomantichoridae, both the wings are rudimentary and in the latter the eyes are much reduced and they are in some cases light avoiding.

In *Platychila pallida* we have only a very slight pigmentation anywhere on the body; the wings are reduced to a rudiment that is barely distinguishable and the elytron is pigmented only in a small area lying in its anterior two thirds and along its inner side. There is no development of spaces in the secondary cuticula sufficient to make the chitin opaque and yellow.

In the Dytiscidae, Carabidae, and Haliplidae, the chitinous columns are arranged in definite rows and likewise in many cases the hairs and glands. The center of these chitinous columns, or better the primary cuticula over the chitinous columns, is last to lose its pigment; accordingly one may find a line of pigmented spots lying in rows, often two rows, between the tracheae, for example as is shown in the *Bembidium versicolor* Lec. (Fig. 35). The row of chitinous columns break across the white markings and in some of our common Haliplidae, for example, the chitinous columns are so arranged and the centers are associated with the openings of glands, the cells of which have caused the column to be cut half in two.

To find what are the conditions of the tracheal structures in other Adephaga I made an examination of a number of forms in the Dytiscidae, Carabidae, and Haliplidae, (Figs. 34 to 41, Pl. IV). Omophron shows all six tracheae and three cross bands which do not appear to be related to the tracheae. *Bembidium versicolor* shows only five tracheae, but the unpigmented areas are in the lines of the tracheae and also between them. *Nebria complanata* (Fig. 37, Europe) shows the tracheae in the lines of pigmentation as well as a suggestion of the double banding shown in the Dytiscidae. The Dytiscid (*Hydacticus stagnalis*, Fig. 38) shows all of the six tracheae and a light line both between and directly above them. Figure 39 (*Laccophilus maculosus*) shows suggestions of cross bands and double stripes. *Agabus teniolatus* (Fig. 40) shows the tracheae within the lines of the unpigmented cuticula. *Hydroporus undulatus* (Fig. 39) has the cross bands and the tracheae apparently between the spots. (Compare with figures 2 to 25, plates I to III).

From the studies preceding, especially the last, it is observed that there is no constant relation between the tracheae and the distribution

of the makings or unpigmented areas, of such a character as to suggest a direct physiological relation between the two. In the specimens in which the tracheae are unusually arranged there is no effect on the color pattern or variation on that suggests a direct relation between the two. Nor is there any connection between the oxygen supply from the tracheae and the pigment. And as the blood sinuses and tracheae are for the most part coincident, I see no reason for relating the blood supply to these characters. The folding of the elytron in the pupa is apparently not related to the cross bands. It accordingly appears that the relation of pigment formation in the elytron to structure is not directly causal, at the present stage in the evolution of the groups but is one belonging to the general structural organization, hereditary in character.

#### THE COLOR PATTERN PLAN

The pattern of the Cicindelae is analyzable into the areas or tendencies shown in figures 42 to 49, plate V. Figure 42 shows the full number of dark and light longitudinal stripes. The light stripes are labeled *a, A, B, C*; *a* is not usually distinct. Very often it is absent as in figures 3, 4, 6, and 11, but sometimes appears to be present without *A* as in figures 5 and 13, plate I and II. It is often present and partially separated from *A* in an Australian species (Figs. 50 and 51, Pl. VI) only. This Australian species is the basis for figure 42. More often it is joined with *A* (Fig. 43), and not recognized separately (Fig. 52). Figure 44 indicates a tendency to double lines between the tracheae suggested by an African species (Fig. 53, also 57 and 7 and 8). Figures 54 and 56 show the longitudinal stripes partially represented.

Figure 45 shows the full number of cross bands rarely complete numbered 1 to 7; but perhaps best represented in figures 57 and 59 to 63 where they occur broken, two spots. Bands 5 and 6 occur nearly complete oftener than 2 and 3 (Figs. 57 and 75). Figure 46 shows the type in which 2 and 3, and 5 and 6 are fused. This is almost a duplicate of the pattern of an African species, figure 58, but also well represented by figures 73 and 74. Figure 47 shows a common type, cross bands 5 and 6 being separate but the more anterior ones being reduced at the anal side of the elytron. Figure 48 shows all the possible spots which resulted from the superposition of the longitudinal stripes and cross bands. There are 19 of these, of which 11 occur in an Indian species (Fig. 62).

Figure 49 shows the spots or elements from which the characteristic patterns of the group are made up. This pattern should be compared with figures 31 to 33, plate III, which show that individual variations follow the rule of the entire group. The usual pattern of *C. tranque-*

*barica* Herbst is seen to be made up of *A1*, *A2*, *B3* (humeral lunule); *A4*, *B4*, *B5*, *C5* (middle band); and *A6* and *7* (apical lunule). In figure 31 may be noted the forward hook-like extension on the so-called humeral lunule which represents *B2*, the union between *B5* and *C6*, etc.

Figures 61 to 72, plate VI indicate some of the commoner combinations of spots. Figure 66 shows a union between the humeral lunule and *A3*; figure 70 a combination of *7*, with *B6* and *B5* which are connected with the central cross band; figure 71 a cross connection in band 2-3 between stripes *A* and *B*; figure 72 a cross connection in band 4 between *A* and *B*; figures 76 to 77, plate VI show the reduction of cross bands to large spots. Thus the conclusion that the patterns are derivable from combination, loss, and extension of a number of inter-tracheal spots falling in cross rows seems justified. There are various types of combination and extension which are not common when the group is considered as a whole, but which represent tendencies in certain isolated groups of species and which must be illustrated (Figs. 78 to 98, Pl. VII) here because they otherwise appear to be obstacles to the plan. One of these tendencies is one toward oblique combinations indicated in figure 78 (a diagram). One type indicated by the wide stippled band is shown in figure 79, a South American species. A similar combination occurs as a variation in an Indian species (Fig. 80). A more gentle sweeping combination is shown by the narrow white line in figure 78 and occurs as the regular pattern of an African species (Fig. 81); shorter curves occur in another African species (Fig. 82). Other oblique combinations are shown in figures 83 and 84. The type of obliqueness shown by several African species (Figs. 85 to 87) is an oblique shifting of the entire pattern; it appears to be turned parallel to the end of the elytron. This appears to be a significant tendency and will be discussed again in connection with the discussion of experimental results.

Figures 88 to 91 show a tendency toward obliqueness of markings reversed as compared with that just described and characteristic of the *princeps-cylonensis* group of India and Africa. It may be said to characterize the patterns of a group standing apart from the other representative of the genus.

Figures 92 to 95, plate VII show unusual sinuate extensions of the markings. In figures 92 and 93, Indian and Australian species, a marking resembling the usual "middle band" arises in the area *A2.3* with a form similar to that found in figures 94 and 95. Figure 96 shows bands 5 and 6 separate toward the outer margin of the elytron and united toward the inner. Figure 97 shows unusual extensions of the markings giving two light bands between the tracheae (compare with Fig. 19, Pl. II); 98 shows unusual direction of extension.

From the preceding discussion and diagrams I concluded that even

the most complicated patterns are reducible to the usual plan or are made up of unusual combinations of spots occurring in other groups of species. Certain laws regarding direction of shifting of markings seem to prevail. These will be noted again in another part of the paper, (page 58).

#### COLOR PATTERN AND PIGMENT DEVELOPMENT

As an example of the usual type of pigment development in *Cicindela* let us follow the events in *C. tranquebarica* (Pl. VIII). In the youngest pupae there is essentially no pigment present except sufficient in the eyes to give a slight brown color. This gradually becomes darker until the end of about ten days when the eyes are a dull brown and the process is apparently complete. At the end of 12 days the tarsal claws, the tip of the mandibles, and the tips of the mandibular teeth have received their full quota of pigment; the pigment proceeds from the tips proximally and by the 13th and 14th day pigmentation is complete. On about the 13th day the distal portion of the tibia of all of the legs show pigmentation on the outer side and this proceeds to the more proximal portions most rapidly on the outside of the leg. The most distal parts of the tibia are pigmented about 2 or 3 days later. Coincident with the development in the tibia is the development in the trochanters where it begins at the outer margin. A slight darkening takes place in the mid-portion of the developing hind wing which is so folded as to make the tip of the pupal wing show dark. At this time, viz., at the end of from 14 to 16 days, the insect emerges. Often at or before the time of emerging the first color centres of the dorsal side of the abdomen have appeared on the last abdominal segment and more rarely also the corresponding centers of the next to the last segment are also present (Fig. 105, Pl. VIII). Usually the animal emerges with the tibia, tarsal claws, part of the trochanters, eyes, mid-portion of the hind wing, and tips of the mandibles pigmented (Figs. 101 and 105a).

The later history exclusive of the elytra is as follows: The pigmentation begins first on the distal joint of the antennae and the maxillary palps (Fig. 101), and on the teeth of the maxillae. After about 8 hours the tip of the inner palp and the ligular portion of the labium shows pigment (Fig. 102); next after about 12 hours the distal segment of the labial palp and the outer wings of the labium darken (Fig. 103). The gula begins to show pigment about as soon as the ligula, and the pigmentation of this part is complete at the end of 12 to 15 hours. At the time (after 12 to 15 hours, Figs. 103 and 107) the general pigmentation begins to be most rapid, pigmentation begins to show strikingly at the proximal portion of the appendages just noted and proceeds to

meet the distal pigmentation (Zeleny, 1907). The extent to which it goes differs in different species and gives a faint pattern to the parts in some species. The pigmentation which begins distally, usually proceeds only through the extent of the more distal segments (Fig. 109 *a* to *e*). By the end of 24 to 36 hours (Fig. 104) the pigmentation is nearly complete by development over the general areas of both body and appendages. Thus in the antenna at the end of 8 to 10 hours rings appear toward the distal end of the three proximal segments, darken and spread toward the proximal ends of the segments rapidly (compare Figs. 109 *c*, *d*, and *e*). The pattern shown in the antennae, legs, mandibles, palps, etc., persist in some species (see page 24).

At 3 to 6 hours after emergence (Fig. 105*a*) the suture between the clipeus and head becomes pigmented. By the end of 8 hours after emergence there are two oblique color centers between the centers of the eyes; these correspond in position to the oblique depressions that occur in the genus *Tetracha*. Beside these there is a center close to the posterior side of each eye, one just behind and inside of this, and one in the middle of the frons (Fig. 106). Pigmentation then has proceeded backward on the clipeus, and backward from the suture of the clipeus on the head (Fig. 106). At the end of 12 to 15 hours, the pigment of the clypeus and anterior part of the frons and centers just described has increased and extended backward, giving a pattern as shown in figure 107. This process continues with general suffusion over the head with the pattern still in evidence at the end of 24 to 36 hours (Fig. 108).

After 8 to 10 hours after emergence (Fig. 106) the posterior border of the thorax shows two centers in the depression at the posterior side. Little change takes place on the under side from emergence. By the end of 12 to 15 hours (Fig. 107) the thorax has presented some new centers, a longitudinal stripe occurs near each margin, and there is a narrower one between each of these and the center, and the anterior depression is darker than usual. The end of 24 to 36 hours (Fig. 108) shows the obliteration of the centers mentioned above by the pigmentation of the inter-spaces.

On the ventral side of the abdomen and thorax pigment begins on the outer side of the more posterior segments first and centers appear from behind forward. During the first few hours the pigmentation does not begin on the remainder of the abdomen. The next center to appear is the one in the center of each segment near its anterior side, which appears between the 6th and 10th hour. Just a little later a line appears across the posterior side of the segment and there is an extension of the center one at each side and the coming in of the a loop-like addition outside of the first center. This system of markings is best

understood by a comparison with the larval segments (Fig. 99 *a*, *b*, and *aa*). If *a* and *b* joined to give the first marking that appears, *aa* standing out clearly and all of the rest joined laterally, one would have the condition found in the development of the adult color.

No change takes place in the thorax except the development of a center of the on the middle line of the meta-sternum which probably represents the attachment of the large hind wing muscles (Fig. 102), until the coloration of the abdomen is has been completed in the ventral side of the third, fourth, and fifth, and last abdominal segments; this having proceeded from behind forward. At the end, 12 to 15 hours (Fig. 103), it will be noted that the hind coxae, the ante-coxal pieces, the episterna of the metathorax and the coxae of the other segments have received a quantity of pigment and a new center has developed behind each metathoracic leg on the metathoracic sternum. The next stage represented (24 to 36 hours, Fig. 104) shows a general diffuse pigment on the entire ventral surface except the outer sides of the metathoracic coxae which long remain unpigmented. The ante-coxal piece is nearest complete. The great possibilities of being deceived as to position of the color centers is shown by the fact that the abdominal centers and center behind the legs on the metathoracic segments is lost entirely in the last stage of the development.

Conditions on the dorsal side are very simple and centers appear just as in the larvae (Fig. 100) two in number on each segment, begin on the last segment, and move forward fusing in the middle line, and in course of about 10 hours after emergence (Figs. 106 and 107) the color of the dorsal side of the abdomen is practically complete.

In regard to the color centers of the ventral side of the abdomen it may be said that they are the same in number and arrangement as found by Tower on the ventral side of the abdomen of the potato beetle larvae. The abdominal centers are serially homologous. The pattern of the dorsal side of the abdomen of the larvae of *Leptinotarsa* is similar to that of the ontogenetic ventral of the adult *Cicindela*. The upper side of the abdomen in the potato beetle larvae is divided with respect to these structures because growth, bulging, and wrinkling due to the extension divide the dorsal side into two parts, and have resulted in the separation of the centers into two rows or bands (see Tower, 1906: Pl. 18). In the larval *Cicindelidae*, however, it is the ventral side that is extended in the process of the development and which may be wrinkled and the centers are separated just as in the case of the dorsal side of the abdomen in the larvae of *Leptinotarsa*. There is never any tendency for the dorsal side of the cicindelid abdomen to wrinkle; in fact it is reduced as compared with ventral. On the ventral side of the adult *Leptinotarsa* abdomen six centers appear but these are not divided as to the middle



of the segment. Tower's basipleural is no doubt represented by the three spots that are near the spiracle (Fig. 99, Pl. VII).

In the prothorax of the tiger beetles it is to be noted that the ontogenetic coloration is parallel to that in some of the Leptinotarsae; the two pairs of parallel lines which occur appear to correspond to markings that are on the prothorax of the *C. tranquebarica* (Fig. 107). The two oblique centers of the frons or epicranium in the Cicindelidae are represented in the Leptinotarsae also the two markings by the eyes.

I have noted that in the antennae centers arise in the form of rings around the distal ends of the 2d, 3d. and 4th segments (Fig. 109 *c, d, e*). Conditions in figure 109*d* and *e* show patterns in the development of these which are the exact duplicate of the patterns in the antennae of the *C. strachani* (Africa) which has also a primitive elytral pattern. *C. theratoides* (New Guinea), many of the Megacephalidae and some Collyridae.

The development of the pigment in the legs up to the time of emergence is described above; after emergence the development proceeds from proximal to distal in the tibia and in the same succession in the tarsal segments. Previous to emergence the humerus is somewhat compressed and wrinkled, being only about two-thirds as long as after the expansion which follows emergence. At the end of about 8 hours one finds the femur beginning to show a general suffuse pigment which appears to arise simultaneously over the entire surface. After this the later history in the legs is simply a general intensification of the pigmentation.

In all of the species of Cicindela studied the phenomena of pigment development are the same so far as has been noted above with the exception of the *punctulata* and *lepida* in which the first centers appear in the middle of the ventral side in the third and fourth abdominal segments. This is the case in *T. carolina* in which the centers are like those in the larvae. The adult abdomen in this species is not pigmented toward the posterior end of the ventral side while the upper side never receives any pigment at all and the usual larval color center are, as has been stated, very much reduced in this species. Likewise the centers of the head and prothorax are little developed and the oblique ones near the center of the frons are very faint. The two which appear first in the posterior depression of the prothorax are quite distinct and very suggestive of the condition in the *Megacephala (Phaeozantha) klugii*. The legs are, however, not pigmented at all and it appears that the cuticula in these cases is of the type with interlamellar spaces which is a means of giving strength to the less rigid parts of the body.

An examination of stained whole mounts of the appendages shows that as a rule the distal portions are first clearly differentiated and

first to take on the form that the part is to have in the adult. The tip of the mandible is the first to show the distinct pointed form toward the head, tooth after tooth being differentiated from the somewhat larger mass of tissue which makes up the mandibular outgrowth. The same is true of the other mouth appendages, labrum etc., they become more hairy in form and stand well separated from the old pupal skin. In the case of the leg the tarsal claws are the first differentiated and this process appears to move in a general way toward the body, segment by segment, the femur being last to be differentiated and last to receive the pigment. The position of the pigmentation in the tibia corresponds to the point of attachment of the flexor of the tarsi. This is early developed and thus the tarsi are the first to become movable; at this time the flexor and extensor of the tibia are not well developed, their muscle striations appearing indistinct, but become much more distinct and definite in form a little later and the tibia becomes movable about the time of this development of its pigment. A similar development occurs on the proximal portions of the trochanters which are the attachment of the muscles. The wrinkled condition of the femora helps to give it rigidity and the legs are well enough developed to allow of sufficient movement to release the animal from the pupal skin. The legs are at first somewhat extended and subject to a considerable amount of movement, and while the body is flexed and extended and the pupal skin ruptured in the midline of the thorax the mandibles are then worked as well as the other mouth parts and the head removed by repeatedly throwing it backward. The animal gradually wriggles out of its skin and the wings and elytra soon expand; the wings expand to the full length inside of about 20 minutes after the animal emerges, and remain thus for several hours. If for any reason the expansion of the wings or elytra is interfered with, they always remain in the exact condition in which they were placed by the adverse conditions, and if the wings are not folded in the normal fashion at the proper time, they will always remain completely extended. Their early pigmentation, if it is associated with hardening, is probably an advantage to this process of withdrawal or folding.

It seems altogether probable that the peculiar manner of development of the pigment is associated with the development of the structures which are necessary to ecdysis and that they accordingly represent developmental adaptations. In the case of the tiger beetles which do not have the appendages pigmented in the adult the cuticula must harden without being pigmented.

The animals emerge with the elytra entirely unpigmented and during the first 4 to 8 hours little change is easily noted. One can hardly record the beginnings of the pigmentation as this is very faint, and the

wings beneath, which come between the elytron and a part of the pigmented abdomen, give no opportunity for accurate observations with the elytra in position except as one slips pieces of paper under them, which may injure the elytra so as to give abnormal development. The elytra must be removed and mounted in glycerine jelly, or cleared in balsam. It is necessary to hold the slide in position over the surface of a good glass plate that has been painted white on the lower surface and not magnify them or if so, only about two diameters with a reading glass. The fresh, unmounted elytra may be placed in formalin in a watch glass painted a neutral gray or yellowish tone which is the same color as that presented by the elytron before pigmentation when viewed in transmitted light. By this method and with individuals killed at different stages, and with the use of a Zeiss binocular microscope, I have been able to follow the course of pigmentation of the elytra. The elytra have been examined in cross section; there are no thickenings in the primary cuticula in which all the pigment is located, except the small thickenings that have been described as occurring in the area immediately in front of hairs, and these have been carefully considered and their relative number as effecting the color effect practically eliminated. The cuticula is somewhat thinner at the tip of the elytron. The actual hairs present are surrounded by an area that is fully pigmented, but this also has been taken into account. Elytra of *C. repanda* show beginnings of pigmentation which often are strongest near the costal border at the end of 4 to 5 hours (Fig. 111). The chief of the areas showing lack of pigment are in the lines *A* and *B* and are particularly prominent near the base. Later (Figs. 112 and 113) these lines are broken into spots which correspond to spots found in certain Eurasian and African species (Figs. 147 to 187, Pl. XII, and 241 to 280, Plate XIV). The series of stages that I have had has been small and not suited to the detailed comparison as some of the following species are, but shows the same thing.

The color development in *C. lecontei* Hald. begins very faintly apparently at about the posterior end of the anterior third of the elytron at first the permanent markings are difficult to distinguish, but a little later they become distinct patches. Two ontogenetic markings between the base of the elytron and the general arrangement of pigment at the end of 4 to 5 hours (Fig. 114) correspond very closely to conditions found in *repanda*. Longitudinal, heavily pigmented stripes that stand out in some individuals, lie in the lines of the tracheae and hairs, and become more pronounced as the development continues. Figure 115, 12 hours after emergence, shows none of the spots characteristic of the others shown but has indications of a cross band which never occurs in *lecontei* but which is present in *rugifrons* and *modesta* of the Atlantic

coast. Figures 116, 117, 118 show a number of spots arranged in longitudinal rows. A comparison of these with figures 156 to 177 and 244 to 261 will make clear a close correspondence between the spots appearing and those in adults of Eurasian and African species. Pigment fails to develop when the elytron is wet (Gortner, 1911). This happened in practically all wet elytra of this species and very few of those in other species.

Development of pigment in the hind wings begins a little back from the anterior end, and in this case, about the time of emergence (Fig. 119), in the region in which the folding occurs, and shows while the wing is in the pupal skin thus causing the tip of the pupal wing to look black. Pigment passes out along the veins in both directions and vein after vein is pigmented toward the anal border. This process requires several days for completion. Figures 119 to 122 show the wing from the time of emergence to the end of about 24 to 36 hours and the adult.

Development in *C. purpurea* Oliv. var. *limbalis* Klg. (Pl. X) perhaps shows more definite spots than any of the others. The first evidences of the pigmentation in ontogeny is in the small circles around the hairs on the elytron; this takes place about 3 hours (Fig. 123) after emergence.

At the end of 8 hours the pigment usually begins to come in generally, first, in the lines of the tracheae. As in the case of the lecontei the first trace is at the posterior end of the anterior third of the elytron. The principal early developmental markings show as large light areas (Figs. 124 and 125, after 8 to 10 hours) which seem divided again later (Figs. 126 to 129, Pl. X) and correspond to the spots found in old world species, figures of which have already been cited. Heavier pigmentation often persists in the line of the tracheae even in the adult (Fig. 130).

In *C. tranquebarica* (Pl. X) the pigment begins first a little behind the anterior end, as in the other species, and comes in the lines of the tracheae with all of the bands represented and the spots growing smaller and the longitudinal stripes less and less prominent as time goes on. In all the elytra, however, the same markings appear as in the other species (Figs. 131 to 134), and spots occurring in other species are consistent in occurrence.

*C. punctulata* (Pl. XI) begins pigmentation about 4 to 6 hours after emergence and the pigment appears to pass from the anterior to the posterior end of the elytron. Certain lighter areas appear especially at the base of the elytron and between the tracheae, figures 135 to 137. These represent cross bands and other bands occur further back appearing in some cases but all are comparatively indistinct. There is, however, a different phenomenon such as occurs in some of the Dytiscidae,

e. g., *Lacchophilus maculosus* (Fig. 39, Pl. IV), a concentration of the pigment around the markings. Even where the markings are absent or almost so the denser pigmentation is present. This seems to have obliterated ontogenetic markings as they are shown less plainly in these species than any other studied. Such spots occur in some species of *Cicindela* as for example *campestris*, *aulica polysita*, *latreillei* (Fig. 257, Pl. XIV) and *ismania* (Fig. 366, Pl. XVI), which have a more densely pigmented spot in the region of the sutural spots of other species, i. e., in the position of *C*2.3 (Fig. 48, Pl. V). In cleared elytra of *campestris* a dark area appears at this point. Elytra of *C. limbalis* (Fig. 127, Pl. X) shows this. In some cases dark spots appear at this point in surface view; in others metallic spots. When the dark color occurs, the conditions described in page 51 are reversed—the surface film is absent. The distribution of the chitinous columns above which areas are first pigmented makes the study very difficult. The hairs on the elytron which lie in the lines of the tracheae show pigment around their bases by the end of 3 or 4 hours if not earlier. The elytron reaches the adult color so far as pattern is concerned at the end of about 15 hours, but pigment continues to be deposited for several days.

Only one stage of *C. sexguttata* (Fig. 138) studied shows the spots in the area between the tracheae faintly. The pigment is piled up about the markings only to a slight degree. *C. punctulata* and *sexguttata* belong to one of the Mexican groups and differ from the other species studied.

One specimen of *Tetracha carolina* (Fig. 139, Pl. XI) was studied; in this the pigment began to develop at the end of about 9 hours and to manifest itself at the outer side of the elytron where it bends under, and appears to move toward all parts of the elytron from there. A somewhat lighter streak was left, however, between the costa and the subcosta tracheae; this corresponds to stripe *a*, figure 139. The pigment moves toward the inner angle but shows a lighter space at the base between the ramus and the media and also a longitudinal stripe between the media and the cubitus, which is broken at a point corresponding with the dark band *B* between 2.3 and 4. This same break occurs in the area between costa and subcosta. That portion of the tip of the elytron between the media and the suture is the last to be pigmented. Figure 140, which represents the elytron at the end of 9 hours shows adult coloration. The darker dots represent the chitinous columns over the center of which the primary pigmented cuticula is thicker than anywhere else. At the point where it has been stated that the pigment began developing the cuticula is somewhat thicker than elsewhere.

In *C. hirticollis* (Figs. 141 to 145) the pigment appears to begin almost uniformly over the elytron except for the weaker places representing the ontogenetic markings. The lighter places are between the lines of the tracheae. There are cross bands at the base of the elytron, the middle one usually more or less clearly connected with the distal end of the adult cross band 3. Usually there is a spot opposite the end of this band between the media and the cubitus and usually another set of dots stretches across the elytron between the band 2 and band 4. These bands of a secondary nature are not present in the later stages or if so not marked. The longitudinal lines become weaker as time goes on and the markings, except those that are to be permanent, gradually disappear; those in the region of the base are last to go. In some cases lighter longitudinal lines are divided into spots.

A late stage in *C. 12 guttata* shows the same longitudinal stripes and cross bands. Throughout the series *longitudinal stripes* seem to be most marked in the earlier stages but become partially divided later and are rarely or never continuous but nearly always broken into spots. This is shown in nearly all the figures presented and the conclusion which seems warranted is that the longitudinal stripes are a more definite character than the cross band, though neither occurs alone. The fact of a combined cross and longitudinal system of unpigmented areas is the one which comes forcefully forward in the entire study though there are irregularities present. Further, one sees a close resemblance between the ontogenetic patterns and those of the African and Eurasian species on which the analysis of the pattern was based. One notes also the close correspondence between the spots shown in the general plan presented in figure 48, plate V, and those occurring in the ontogeny of the patterns of common North American species. This would seem to establish the plan of the pattern as well as could be hoped.

The entire set of evidence presented tends to show that the simplest type of pattern in the Cicindelas is a pattern of spots lying in lines between the chief longitudinal tracheal trunks and falling into cross bands of which there may be seven. In ontogeny these are subject to some variations but such a description fits the general relations found better than anything else that can be stated. Such a type of pattern, which is of the character that is commonly called primitive, is what might be expected among insects. The wings are usually characterized by longitudinal veins which are thickened and hardened and often pigmented. These veins are connected transversely by cross veins which are much more diversified in the insect group than are the longitudinal ones and which are also much more subject to individual variation. Tracheae usually occupy the longitudinal veins but not always the cross veins, hence in the insects which have actual cross veins there is not a neces-

sary correlation between the veins and the tracheae. The greater hardening and more general pigmentation of the veins of many insects already mentioned (page 16) leads to a spotted type of wing, in many cases at least. Such a system offered in the elytra of the tiger beetles gives the basis for the spotted type of elytron which we find frequently in the group. Veins no longer occur definitely longitudinally and the tracheae do not ordinarily bear any definite relation to cross areas.

A large background of evidence is presented above for the selection of the spotted type of tiger beetle pattern, made up of spots falling into rows and forming stripes and rows forming cross bands, as a general one from which other types are derivable *by the loss of spots, combination of spots, etc.* Comparable analyses were presented by Eimer (1895) and Von Linden (1902), who note cross bands as the basis of the patterns of various species of Lepidoptera. Tower (1906) reduced the general plan of markings in *Leptinotarsa* to cross bands and longitudinal stripes. He recognized 4 or 5 unpigmented cross bands and 6 longitudinal unpigmented stripes which fall in the lines with the tracheae instead of between them as in *Cicindelidae*. He shows the stripes divided into two in the area between the costal and subcostal tracheae (Tower, 1906:228, Figs. 5 to 8, Pl. XXIV), which is comparable to the condition suggested in the carabids and dytiscids shown in figures 35, 38, 39, and 40, plate IV. Tower adhered to a theory often held by embryologists, namely that the base of the wing is oldest; further, that pigment appears first in the base of the elytron and proceeds to the distal portion in accord with the relative age. No conclusive evidence is brought forward to show that the base of the elytron is actually oldest, and an examination of Tower's figures (Tower, 1906: 156, Figs. 1 and 2, 7 and 8, Pl. 19) shows that the basal part of the elytron in some species is not first pigmented. Pigment begins in the costal border of the wing and at the level of the second dark cross band which he calls the "proximal" and which is very common in his group. This is comparable to the early stages in *Cicindela* (Fig. 111). The view that pigment comes in first in cuticula over the oldest tissues from the embryonic standpoint seems not to hold good in *Cicindela*, for on this basis certain abdominal sclerites would be embryonically older than others (Figs. 102 to 104, Pl. VIII), the last abdominal segment older than the first, and the femur younger than the tibia as well as other peculiarities shown in figures 99 to 103. The law cannot be said to hold good at all in the group under consideration, but rather as has been noted on page 24, there is an order of post embryonic development of adult organs, which coincides with pigmentation.

One of the most recent color-pattern analyses (Braun, 1914) shows the pattern of *Lithocoletes* (microlepidoptera) to be made up of a mod-

ication of seven transverse dark bands with six transverse light bands between them (page 161). The figure of the hypothetical pattern is in general terms almost identical with that shown for *Cicindela* and independently conceived on plate I, figure 4. In this second and third light band are represented by a single wide one and the fifth and sixth are separate as two narrower bands. If the general plan of longitudinal and cross bands in insect patterns is to be accepted we must also conclude from the evidence presented that the relations to trachea may be reversed, i. e., the pigmented areas may lie immediately above the tracheae or between them. In the Lepidoptera pigment appears last in the veins (Mayer, 1896).

The areas between the trachea may be subdivided into two longitudinal bands. The pigmented and unpigmented bands may also be reversed in position as would appear to be the case when we compare the usual cicindelid patterns with those studied by Tower. There is no reason why this should not be the case as when markings are lost; the pigmentation which results is often heavier than elsewhere (Figs. 135 and 136).

However when one compares the cicindelid ontogeny with the existing patterns of other orders one finds that they show a series of light spots such as might easily correspond to the so-called cells or areas divided by longitudinal and cross veins in a primitive insect such as a may-fly. The may-flies, stone flies and many diptera show such an arrangement in some parts of the wing. At least it may be safely concluded that a pattern of faint spots is the primitive type in Cicindelidae if one accepts any of the current criteria for primitive forms.

I start with this type of pattern as "primitive" with a consciousness of the fact that it would be possible to proceed in entirely different directions and from entirely different starting points and make out cases of modification in definite direction fully as plausible as the ones here presented, provided only the preceding strong evidence is not accepted.

On this account it may be well to give the reasons for presenting this matter of modification at all. First, it is presented to further establish the contentions already made as to the character of the pattern plan presented; secondly, to show that all even the most specialized types of patterns could have been derived from the generalized types described above; thirdly, to show that there are certain laws of modification which must have been very general in the group and which have operated again and again in the production of the characteristic types of patterns.

Figures 149*b*, 156*a*, and 165, plate XII, show some of the patterns in which five nearly complete cross bands occur; 179 shows a very



simple band, 1 with a complete, 4 etc.; 185 shows a wide cross band representing 3 and 4. Figures 149*b*, 149*a* and 156 represent the patterns of an African species showing that variations are in the direction of greater obliquity of the cross markings, 149 approaching very closely to 148, which is a different species and usually oblique. A third species is strikingly oblique but still possessing the usual cross bars of the group of species. Thus in this small group the usual typical pattern as shown by the general observations preceding is decidedly distorted by in a definite direction.

In figure 165 is shown a type of pattern in which the cross bands are nearly vertical to the inner line of the elytron; all the spots present fall in to such bands as they do in the ontogeny series (Figs. 112, 113, 116 and 117, Pl. IX; 128 and 133, Pl. X; 143 to 146, Pl. XI). In all the other figures on the upper half of the page the two spots near the elytral suture are not in line with the cross bands. Evidence of this will also be found in the ontogeny series but is less marked than the tendency toward transverse bands. In 165 and 165*a* and in 156 and 156*a*, plate XII, the components of crooked middle band are clearly brought out in course of variations in which two bands may or may not be joined in the stripe between the media and radius. This tendency should be noted as the most characteristic of the genus *Cicindela*, as there is scarcely a group of species as arranged on the basis of pilosity by W. Horn in which some one does not show this type of joining. The breaking of the cross bands by pigment in the line of the media is also very characteristic, but the tendency for the spots to lie out of the lines with the cross bands as interpreted, is taken as evidence of one of the general tendencies to be discussed later. The relations of the characteristic patterns to the general plan is thus made evident. Another general tendency also manifested is the tendency for the spots shown in figure 156*a* to spread and join, not in any direction but in definite lines. The figures to the right and above figure 165 illustrate the tendency for the markings to join in the line between the pigmented areas of the media and cubitus and for the individual markings to still retain their characteristic form. On this basis the unusual and aberrant patterns such as 150, 151, 152 and 160, 161, 167, plate XII, are easily explained. In spite of the extreme extension they are like 157.

Figures 170 to 187, plate XII, show the patterns of species in which the longitudinal striping has been developed chiefly in conjunction with some cross bands, but in which there is no suggestion of the characteristic middle band. Figure 169*a* shows the pattern of an Australian species in which all the dark and light longitudinal stripes are represented. The dark area over the subcosta is clearly distinguishable. In 169*a* this subcostal dark stripe is reduced but still present.

Figure 169 shows the extreme extension of the white; 168 shows a reduced pattern of the same type; 175, a species with three represented simple stripes; while 183 has only one stripe; 170 and 170a show the variation in one species in which the middle white stripe may be either present or absent, and the two posterior cross bands are present and curved like the end of the elytron. In 171 the cross band is broken away from the innermost longitudinal stripe in the area of the dark line of the media trachea; 172 shows a wide middle band with the longitudinal stripe represented only in the anterior portion. Figures 173 and 174 show types with connections between an outer, unpigmented side and the central light stripe in the center. Figures 177, 178, and 171 show a combination of the lateral stripe and the cross band 5.6; 180 to 181a show patterns which may have arisen from types like figure 158 above. Comparing 177, 182, 184, 184a, and 176, one notes varying lines of oblique connection to which attention was called in figures 78 to 87, plate VII. Figures 188 to 231, plate XIII, show cross bands in the Indian-African-Australian group in which reversed obliqueness of the central band 4 is developed. This obliqueness is rare outside this group except in forms with a well developed sinuate middle band (e. g. Figs. 292 to 298, Pl. XV). Figures 188 and 188a show the well developed cross bands, 1 and 2.3 being joined at the side; 189 is similar and 1 and 2.3 are joined obliquely; 190 is similar but reduced. 198 and 199 are similar to 188 but have lost the last cross band and further reduction in the same direction would result in patterns like 197, 205, and 206. 191 to 196 show a series based on the central white stripe variously broken into spots representing cross bands. 200 to 204a and 213, plate XIII, are a series of related species occurring in India which show an unusual oblique arrangement and combination. 209 an African species belongs to a group with pilosity similar and closely related to the Indian group including 201 to 204a; it shows the same type of obliqueness in the central marking as in 200. 210 to 212, plate XIII, show further modification of the central band and connection with the oblique humeral curve in the line of the central light space. 220 shows a slightly different trend of similar elements which give the combination in 221 or 220 and 219, depending on the trend taken. 214 to 218 and 222 to 231 show the simple patterns of cross bands in which the last and usually the first are missing. 232 to 240 show combinations of markings resembling those just noted in *Cicindela*, in *Therates*, *Prothyma* and *Odontochila*; compare 232 and 197, plate XIII; 233 and 206, 234 and 197; 235 and 219; 236 and 219; 237 and 188; 238 and 239 with 210 and 213; and 240 with 188. There are resemblances between patterns in other genera and those in *Cicindela*.

One note-worthy African species (Pl. XIV, Fig. 242—compare

with 209, *C. oscari*) shows the unusual oblique bending of marking which characterized the group noted above. This and *oscar*i are however the only species in which it occurs and the group to which it belongs is similar in pilosity to the Indian groups just described. This particular one stands in closest relation to those shown in plate XII, figures 170, 170*a*, and 171. It is introduced here because at the *outer margin* its markings represent 2, 5, and 6 with the almost universal central or fourth absent, except at the innerside where 4 seems to be present and obliquely joined to 5. 241, *a* and *b* show a pattern in which 5 and 6 are present while 4 is wanting except for a few small dots. This species appears to show a tendency to double longitudinal lines. 243 shows a second African species in which there is a tendency to double stripes but the central cross band represented at the margin. The patterns show in figures 244, 244*a*, 245 and plate XIV are of especial interest because the division of the second cross band in those numbered 3 and 4 in the preceding figures are both represented as spots. This is of rare occurrence, the more usual arrangement being like that shown in figure 251. Figures 248 *a* and *b* show the double longitudinal stripes of an African species, a case similar to those illustrated above in which one of the types of variation is in the direction of the spreading of the white. Figures 247 and 247*a* show the joining of such markings as occur in 246 and 259 to make a central longitudinal stripe.

Figures 257 to 261, plate XIV, show unusual patterns of spots, which fall into the usual cross bands on the whole, but those in the inner margin of the elytron are usually shifted out of line. Figures 262 to 280 show various directions of reduction of markings in patterns of the type shown in figures 266, 274 and 274*a*. Those at the left show the loss of the central stripe and those to the right the loss of the inner markings, entirely or in part. 281, 282, 283 show the extensions and obliquity in the type pattern shown.

Plate XVI, figures 292 to 306, show the American species in which cross bands 5 and 6 are separated as seen in 289, 294, 293, etc. The general tendency is for the markings to disappear from the anterior to the posterior end.

The component parts of the oblique vitta of some species of the Mexican group is illustrated by figures 311 to 313 and 319 and similar components making a somewhat different vitta in 291, 296*a*, and 297. Figures 315 to 328 show patterns in which the last or apical (7) cross band is missing or in which variations arise in which it is reduced.

Figures 329 to 355, plate XVI, show the species chiefly Eurasian, a few American, in which bands 5 and 6 are present and separate, the former illustrated by a marginal spot behind the center. Figure 347 shows a narrow longitudinal stripe extending forward from the spot

near the apex, this is an unusual variation in a race of a European species. Figures 361 to 363 show a tendency in certain species for the formation of a vitta in the space between the subcostal and radius (tracheae). Figure 364 shows an unusual joining of the marking of a specimen of *C. limbalis* loaned by Professor H. F. Wickman, in the space between the subcosta and the radius, though the species rarely has the markings joined and when so not in this line (*A*) but in line *a*. 365 shows an aberrant marking in the central part of the elytron of *C. campestris*, which is a common European species. 366 shows the darker spots about the white marking in a closely related species. 370 to 377 show the patterns of other genera; compare 370 and 362; 371, and 185; 372 with 367; 373 with 367.

Figures 402 to 478 are presented to show series of unusual combinations illustrated by the Indo-Australian group of species. 378 shows a marking projecting backward composed of the band 2.3 and the longitudinal part of the pattern plan which lies between the media and the cubitus (tracheae); the lettered number of the same species shows the extinction of the white. 386 shows an unusual type of pattern in which the curve appears to rise in cross-band 3 while the light stripe between the media and cubitus is obliquely joined in the anterior end to the central spot at the elytral base. Extension of the white is common in variations in this group (383, 384, 385), 379 to 382 show a combination between the middle band and the central basal spot and spreading of the white. 389 shows a similar pattern but with the joining in the cross-band 2.3 and extension of the white. 387 and 396 are somewhat generalized, representative of the type in question which with slight modifications may have led to the 397 and 398 series of patterns (*f*) or by extension to the 392-395*a* series and 400. The balance of the illustrations show the unusual patterns of the *Cicindelas* both reduced to a single marginal stripe and in full form. Most of the species represented are from Australia and New Zealand.

Figures 422 to 454, plate XVIII, show the unusual marking of *Cicindelas* with slight distortions, but all the patterns belonging to groups of species which show a strong tendency in the chief representatives to vary in the direction of nearly all white individuals. The irregular and oblique marking in figures 422 and 423, representing two South American species, shows an unusual type of degeneration of the system. The peculiar irregular, branched and scattered character of the markings of several groups shown indicates the breaking up of the system of marking which has been designated as the type upon which they are based.

The different species are characterized by peculiar turns forward

of certain markings. Compare for example the anterior cross-band (humeral lunule) of 436 and 427; one is turned forward with a characteristic curve, the other backward. This is a difference between the two species which holds good throughout all the individuals. The extension of the white shown is clearly associated with a degeneration of some of the chief tracheal trunks.

From this large series of figures we must not permit ourselves to judge that all types of pattern are equally common and equally general in the species of the genus. Figures 329 to 333, and figures 130 and 131 show the commonest and most characteristic types in the genus which are universally distributed and make up vast majority of the grand total for the world.

This, the first definitely directed tendency in the group, has been the union of spots to form the characteristic markings of the group shown in figure 49, plate V, as combination of *A1*, *A2*, *B2*, or *B3* to make the *humeral lunule* so called, of *A4*, *B4*, and *B5* to make the so-called *middle band*, and of *A6* and *7* to make the apical lunule of the taxonomists of the group. If these three types of joining are granted as the first directive principle entering into the make up of the patterns of the group it must also be noted that it does *not* apply to the majority of species in nine of Horn's groups (XXVII-XXXVI) including 40 species (Figs. 188 to 215 and 220 to 231, Pl. XIII). A few patterns with middle band and apical and humeral lunules, and which have three spots in the basal and anal portion of the elytron, are included in these groups and differ from most others of similar components in the *presence of these spots* (Figs. 273 and 274, Pl. XIV, and 163 and 164, Pl. XII). These few are the only representatives which show this characteristic middle band humeral and apical lunule. It applies to only 16 species of the Horn's pilosity groups XVIII to XXII which include 66 species in Africa (Figs. 147 to 149*a*, Pl. XII; 269, Pl. XIV; 156, Pl. XII; 265, 241 to 272, 278 to 280, Pl. XIV). Of the figures cited, 156 and 265 are of the most primitive type and 266, 267, 275 and 278 show modifications.

If we grant the majority of the remaining 500 species show these characteristics as variations or that they may for purposes of discussions be assumed to have been derived from forms which did have the three characteristic markings we note that in general the patterns except those mentioned above fall into two parallel series one without the spots, including the majority of species, and the other with them, including a comparatively small number of species. Those with the three spots are confined chiefly to the land directly bordering the Indian Ocean being especially numerous in Africa and India. Spots may be wanting in some variants of such species as *escheri* (Figs. 267 and 268)

and *monteiroi* (Figs. 276 and 277). These belong to groups which normally have them, but they almost never occur in groups which do not show them in a majority of members. Considering the components of the three spots, the anterior central spot (*B1*, Fig. 49, Pl. V) is a part of the basal cross band *1* clearly shown in figure 179. The anterior one in stripe *C*, figure 48, plate V, appears to be a fusion of spots *C1* and *C2* and the posterior one of *C3* and *C4* as a rule, though sometimes the posterior one is *C4* and the anterior one *C1,2*, figure 165. There is a tendency indicated by variation to drop out these markings in many species. In *flexuosa* usually *C 1,2*, i. e., the basal sutural spot, is first to go. In others this is not true as a rule, as shown in 261, 276, 277 and 280. On the other hand there is no species in which these are present and other markings absent. These facts indicate that these spots show a tendency to disappear first, leaving the types of pattern without them. More rarely they may unite to form a band which may persist in the extremely modified forms, figures 151, 160, and 167. One of the characteristic types of marking which seems to belong to almost the entire group showing the typical middle band, is the oblique shifting of the cross band which makes the *humeral lunule*.

The tendency toward obliqueness of the middle band of the typical forms seems quite general in many groups but by no means universal, and is shown by some species in all the groups, and hence is illustrated in all the groups of figures: 157, 163, 222, 227, 273, 276, 288, 299, 451, 335, 336, 342, 411, and 417.

In other groups another tendency seems to be present, namely toward a sharp forward-bent angle on the middle band (Fig. 482) figures 209, 206, and many others in which the usual combinations have not been affected are shown in plate XIII. On the other hand scarcely a species in plate XII shows this tendency except figure 150. Figures 292 and 293, plate XV, 339, plate XVI, and others related show the same tendency. It is shown in the patterns of the Australian group (Figs. 394 to 396, Pl. XVII) where a middle band involving different elements occurs, and is particularly conspicuous and characteristic in some of the Mexican and South American species (Figs. 428 to 434, Pl. XVIII) where it is the chief distinguishing feature. In the group as a whole the most striking tendency is for the markings to disappear beginning in the proximal anal region of the elytron and usually leaving the more posterior distal markings present. But to this there are many exceptions in which the central marking on the elytron is the only one left. (See figures 255, plate XIV; 222 to 231, plate XIII; and 206.)

Another tendency manifested in many species is the extension of the white; it is seen to crop out in all groups from any starting point which is in existence and to proceed from the spots characteristic of

the group, in the direction of general concentric extension in which the original type of pattern may be recognized (Figs. 160, 167, 169, and 181, Pl. XII; 204, 204a, 196, Pl. XIII; 378 to 437, Pls. XVII and XVIII).

Thus one who inspects the figures as arranged, is impressed with the fact that there are a great many directions in which patterns have been modified and these figures are numerous and intentionally substituted for less satisfactory descriptions. The material afforded by the 600 or more species is rich in possibilities and excels in this respect the butterflies of Eimer or pigeons of Whitman.

#### EXPERIMENTAL MODIFICATION OF PATTERNS

To test the laws of modification of the typical patterns of *Cicindela* larvae of several species—*C. tranquebarica*, *repanda*, *hirticollis*, *limbalis*, *lepida*, and *lecontei*—were subjected to low temperature, high temperature, and moist and dry conditions. The temperature was raised about 10 degrees C. above that encountered in the normal outdoor life history. The experiments were carried on in the apparatus shown in figure 455, plate XXIX, and described in connection therewith.

The larvae were put into the high-temperature (near 37°, 1906; 40°C, 1905) about May 15. They were placed in a lamp chimney containing fine sand. The apparatus as arranged gave 2° to 4°C. higher temperature at the top than at the bottom. The average of the two was used in computing the mean. Temperatures were taken twice a day as a rule. The temperature rose each day as the sun shone on the cases so that during the hottest weather daily maxima in soil temperature went to 40 to 42 degrees at times.

The results of the experiments on *C. tranquebarica* so far as the patterns are concerned are shown in figure 456 *a* to *g*, plate XX, and 457 *a* to *b*, 458, 459 and 460; these should be compared with control 456 *a'* to *b'*, *w'*, 457 *a'* to *e'*, *w'* and 458 *a'b'*. A comparison of these experiments with their control and the representative of the forms collected in the field from the same generation shows that in the controls the normal middle band reaches to the margin of the elytron where it is expended in the line of the longitudinal band *aA*; the longitudinal part is parallel with the anal side of the elytron; the middle band is hooked at the end or turns into a horizontal position in compliance with the normal direction of the transverse band from which it is derived. The humeral lunule is usually hooked. The angle in the middle band is a right angle and there is a forward extension of the middle band at the angle.

The patterns which result from the experimental conditions almost without exception differ from the control in the following respects:

1. The humeral lunule is usually without any enlargement at the end suggesting an expansion in the place of spot *B*<sub>2</sub> and 3.

2. The middle band is withdrawn from the margin in all cases and in only one case, figure 556 *g*, is there any longitudinal extension.

3. The angle of the middle band is always less acute and the forward extension less pronounced.

4. The longitudinal portion of the middle band is oblique to the anal or inner margin (suture) of the elytron.

5. The end of the middle band is not hooked but rounded, and rarely even parallel with the transverse bands.

A close examination of the marking of the experimental individuals show that there is correlation in all the respects in which the middle band is modified, in general the most oblique middle band is almost withdrawn from the margin and shows least hook at the end.

Figure 461 shows an unusual type of marking and of modification, the most reduced marking in specimens of *C. limbalis* subjected to the same experimental conditions as the *tranquebarica* shown above. The usual type of modification which is quite general in experimental specimens has the longitudinal portion of the middle band shortened. It is also more oblique and thus less like the simple type. The middle bands of these specimens approach those of the variety *splendida* (Kansas). They represent a more extreme modification of the simple type than the experimental middle bands of specimens of *C. tranquebarica*. The markings in two out of about twenty individuals (Fig. 461) surviving the high temperature showed a sharp bend forward. This is the reverse of the usual tendency in the *purpurea* group but is a strong tendency in some other species shown in plates XIII and XV. One individual out of several hundred collected from the habitat in question, reared as controls, and reared for ontogeny showed this character. Apparently the tendency to respond by a sharp forward bend is little developed in *purpurea*.

Figure 463 *a* to *d*, 464 *a* to *c*, and 466 show the patterns resulting from the high temperature experiment with *C. lecontei* while 466 *a'* to *c'* and 467 *w'*, *x'*, *y'*, and *z'* show the control which survived and the range of variation in a series of specimens collected from the same area from which the larvae for the experiments were obtained. First of all the high temperature experiments show patterns with reduced markings. The markings shown in 463*a* are joined in a way which rarely or never occurs in the stock from which they were collected and which is on the other hand characteristic of the varieties of this species which occur on the Atlantic coast. Also 463*d* shows a pattern which is smaller in markings than any that have ever been collected near Chicago,



467 *y* representing the smallest, which makes the marking of 463 undoubtedly reduced by experimental condition.

Figures 465 *a* to *b* show experiments in which the larvae pupae were iced from the beginning of the pupal stage; all either by remarkable accident or through the effects of the experimental conditions show the widest type of markings; a third specimen was only slightly modified. In 465*b* the form of the end of the elytron is rounded in an unusual way and the surface appearance of the entire body and the elytron are different from the normal types.

Figure 468*a* and *w'* show the type of modification occurring in experiments on *C. hirticollis*. The middle band is modified as follows: the hooks and angles are rounded, the transverse part which usually turns forward and has a sharp angle as in 468 *w'* is oblique in the opposite direction. These modified patterns are identical with those in southern and western localities. This modification is of the same kind as that in *C. tranquebarica* and *C. purpurea*.

Thus it is evident that *C. tranquebarica*, *hirticollis*, and *lecontei* may be modified in structure and pattern by high temperature during the pupal and prepupal stages. Experiments performed on *C. repanda*, *lepida*, and *punctulata* show no such modification, or pattern modification of any other type so far as has been noted. Specimens stimulated by a temperature of 37°C. in the fall and forced through the winter were modified only in case of the specimens which emerged *early*, January 1. Specimens which emerged in the spring earlier than the normal were not modified. One specimen of *C. hirticollis* (Fig. 566, Pl. XXXI) coming through without any winter was very much smaller than the normal. A specimen of *C. lecontei* shown in color plate XXIX, figure 556, was different in form, the abdomen being broadest at a point not usual for *lecontei*.

One of the patterns of *tranquebarica* produced in this way (Fig. 459) was one of the most striking modifications obtained.

Thus so far as the species which show modification are concerned the modification appears to be in *definite directions* and the modifications of *C. tranquebarica*, *C. hirticollis*, and *C. limbalis* are in the general direction in which the modification of the pattern plan has proceeded in many patterns which have deviated from it in course of their evolution. The experimental results further show a basis for the interpretation of the geographic variation of the group which is our next topic for consideration.

#### GEOGRAPHIC VARIATION OF PATTERNS

*C. tranquebarica*, very widely distributed in North America, (Pl. XXII) shows great variation in color and markings, but the

extreme forms are comparatively rare and confined to the Pacific states. Plate XXI shows the classes into which the patterns of this species may be divided and their distribution. The graphs represent the distribution of the per cent of classes shown by the figures below for specific localities. It will be noted that types *g* and *h* which correspond in middle band characters occur occasionally as extremes especially in Kansas and Texas localities, while west of the Rockies where the summer and springs are dry and favor high soil temperatures these types are fairly common. This type of marking with middle band reduced at the margin makes up a considerable percentage of the individuals collected at Hagerman, Idaho; San Bernardino, California; Provo, Utah; and Las Vegas, Nevada; but they are nowhere the dominant type. In certain Nevada localities the retirement of the middle band appears to begin at the inner end and the withdrawal from the margin follows only in very reduced types. The type with the middle band withdrawn occurs in southern and western localities. Twelve per cent of the specimens from central Texas show middle bands like those modified in experiment. On the whole there is a correspondence between high soil temperature and the reduced type of markings which accords with the experimental results.

Plate XXIII shows the geographic variation of *C. scutellaris* and its varieties ranked as aberrations by Horn. The series of classes shown beginning at the extreme left are from the northern portion of its range in New England; passing to the right are shown very reduced markings at Raleigh, and very rarely any markings at all at Mobile and in Texas localities or points in western and west central states: Oklahoma, Kansas, Nebraska, and South Dakota, Colorado and New Mexico. In all localities, however, on and east of the Missouri River in the central states, there is a noticeable increasing in the size of markings as we pass to more northerly localities and to more easterly localities as far as Chicago. East of Chicago the marking of specimens from along the lake shores are not larger than those taken at the south end of Lake Michigan. As will be seen from the graphs (Pl. XXIII) the range of variation is least in the gulf states localities where the markings are most reduced.

There is further a noteworthy difference in the Mississippi Valley and Atlantic Coast forms. The humeral dot (*a1*, Fig. 48, Pl. V) is never present and the so-called posthumeral dot (*A2.3*, Fig. 48, Pl. V) is seldom so except in the more northern localities and is never large when present. It is never joined to the middle band (*A4*, *B4*). The markings are massed in the posterior half of the elytron on the costal margin. In the forms from Missouri River localities and eastward the humeral dot is usually present—always present in the more eastern

form—and its absence is associated with extreme reduction of the markings in general. Thus patterns made up of a row of dots on the costal side of the elytron are the most numerous in Iowa localities and probably those just east of the Missouri River. Thus the selected classes of individuals are geographic in their relations and hence true classes. Further evidence for this statement is shown in plate XXXIV where the color differences are indicated, showing that the immaculate forms are further divided into races on the basis of color. Those of the humid southern states are green, and those of the western steppe, with its dry early summer following early spring rains, are red.

In full accord with the experimental results cited above are certain differences in patterns of two localities from which collections were made often. The larvae used in experiments were collected from a point just north of the village of Miller, Indiana, from a small area of oak dunes about an acre in extent. Adults were collected from this same locality during several years at various times in the season and differences in color and pattern were noted. Graph 10 is the distribution of classes in 200 individuals belonging to the generations of 1904 and 1905. This same graph is repeated above on a smaller scale with graph 11 added, which shows the distribution of classes in 51 specimens collected from the same area in April, 1906. Graph 12 shows the distribution of classes in a series of 60 specimens collected in the north-western part of Gary, (600 ft.) (Pine Station, Indiana,) in April, 1906, showing the modal class to be *o* instead of *q* and a small percentage of individuals with markings joined. Graph 13 shows the distribution of classes in a series of 37 specimens collected in September, 1908, in which the same difference is shown. A difference in the distribution of classes is indicated by a comparison of Graphs 12 and 13. These differences are striking for one who is familiar with them. The differences between the Gary and the Miller locality were noted while collecting the species in the two localities during several years. The specimens collected in Gary showed those with markings joined as very rare. The entire series from the Gary locality show the same thing. There are also similar differences from generation to generation, in the catches from Miller. The difference in the conditions at Miller and in the Gary locality is striking particularly during the larval and pupal periods. The area in Gary is covered with scattered pines and in places from which some of the specimens were collected cottonwoods occur. The area is one of lake sand on which cottonwoods grow up and are succeeded by pines and the pines by oaks. The Miller locality is an oak dune area with well-established growth of oaks. One mile south of the Gary locality are oak covered ridges. Specimens from here are of the usual type taken in the Miller locality. Many of the

pinus had been cut off the pine belt in Gary where my specimens were collected. It is about as open as the cottonwood belt where evaporation from the porous cup atmometer is about twice that of the oak dunes in which the Miller specimens were collected. The soil temperature goes very high in the Gary locality.

Distance below surface	Temperature in degrees C Air 36 C
1-4 cm.	47
3-4 cm.	38
8-9 cm.	35
10-11 cm.	33
12-13 cm.	32
17-18 cm.	30

These forms pupate at a depth of 15 cm. and thus at a temperature of 31°C. on the warmest days. The temperatures in the shade in oak covered sand dunes are much lower being about 27°C. under the same conditions.

Plate XXV shows the division of the various subspecies of *C. purpurea* into classes. Here the primary division of the group, shown in the immaculate form in the center of the group which is very rare, is an habitual one—those at the left are the patterns of a series of races which inhabit level ground usually among scattered vegetation. To the right are those that occupy steep banks, particularly clay banks. Classes *a* and *b*, *cimarrona*, and *t*, *10 guttata*, do not appear to be so differentiated and accordingly the graph perhaps should have been reversed with the generalized patterns in the center, though further investigation would be necessary to determine this. The present arrangement is based on resemblances between the two, *cimarrona* and those at the left, and *C. 10 guttata* and those at the right. The distribution of the two groups shown at the right and the left of the center are shown in figures 471*a* and 472.

If one notes the localities represented by the graphs showing the distribution of classes, it is evident that there is no striking difference in the distribution of classes in Puget Sound, Massachusetts, and Colorado. The modal class for Manitoba, Topeka, and Chicago, is the same. This goes to indicate that the main line of separation is habitual rather than geographic.

Similar relation could be shown for other species. The main differences in patterns are primarily associated either with different localities usually separated geographically, or with differences in habitat preference.

The figures on plate XXVIII (Figs. 473 to 536) are arranged

in parallel lines of similar patterns. Thus figures 473 to 485 are patterns of *C. tranquebarica* similar to those shown in figures 486 to 494, excepting 481 and 483 which are different species closely related to *C. tranquebarica*. In figures 486 to 490 are shown a series representing the typical patterns in *C. scutellaris*; it will be noted that these parallel those of *C. tranquebarica* with most reduced markings. Also figures 491 to 496 show the pattern of the Great Basin group of species and varieties to which *C. fulgida* is closely related. These parallel some of the patterns of *C. tranquebarica* and are in turn paralleled by those of other species. Concentric extension of the white likewise characterizes the patterns of the group. Figures 497 to 501 show a series of patterns in *C. pulchra* which are roughly parallel to those of *C. tranquebarica* and very closely parallel to those of *C. scutellaris*. The commonest pattern of this species is, however, figure 498; 499 and 501 being rare and collected only near Alpine, Texas.

Figures 503 to 505 show the series of patterns of *C. longilabris* which parallel the patterns of other species shown above and below.

Figures 506 to 518 show a remarkable and long series of patterns of *purpurea* paralleling the entire *tranquebarica* series without the addition of other species. The entire series is however different than the other series especially different from the *tranquebarica* series because of the short humeral lunule which always stops with spot *A*<sub>2.3</sub> while that of *C. tranquebarica* is made up of *A*<sub>2</sub> and *B*<sub>3</sub> in oblique combination (see Fig. 49, Pl. V). Figures 522 to 527 show the markings of the *C. sexguttata* group which parallel those of the other groups quite well throughout a series of five types. Figures 528 to 536 show a series of types belonging to five closely related species. The patterns at the extreme right show extension of the white which appears to have occurred as a tendency taken at any point in the series represented; thus figures 520 and 521 belong with 488 and to the same species. Figure 519 belongs with 531 and represents a different type of extension.

While a general parallelism is shown by the series of patterns, there is also a characteristic series of small differences belonging to the usual types of most species. This indicates that *specific* characters in the color patterns are matters of detail and any definitely directed *specific* or *racial* tendencies would have to be based on a consideration of such details rather than the general plan of the pattern and the general parallelism shown in the group of figures just discussed. While *specific* patterns are often very closely parallel, one who is very familiar with them can identify the species from a single elytral pattern in the vast majority of cases.

Considering the pattern of the rest of the group, represented in figures 473 to 537, *C. formosa* and its varieties is distributed on the

Atlantic coast and for some distance inland in Massachusetts to Maryland where the markings are of the type shown in figure 532 and slightly wider with the all joined at the side. The sharp forward bend of the middle band is characteristic of the eastern forms. *C. formosa* is distributed about the sand dunes of Lakes Michigan and Erie and through the sand areas of the central states, the distribution being very nearly like that of *C. scutellaris* except that *formosa* is wanting from Virginia to Texas along the Atlantic and Gulf Coasts.

The markings of the western Mississippi basin forms are broad as shown in figure 531, plate XXVIII, while in the more southern and western forms from Texas, Colorado, and Oklahoma are characterized by a middle band tending to be straight across the elytron.

The species which stands close to this is *C. venusta* (Figs. 533 and 534). The pattern is similar to that of *C. generosa*. It occurs only in sand areas of the great plains. The southern representatives have markings similar to figure 531 in width, but in Manitoba there is a tendency to the extension of the white as shown in figure 534. *C. limbata* is a closely related species which is taken only in blowouts in sand hills of the western Nebraska region and of Manitoba. Figures 535 and 536 show typical patterns. They do not vary greatly geographically.

*C. ancosisconensis* and *duodecemguttata* are invariable species (Figs. 528 and 529), *repanda* a subspecies of *12 guttata* distributed almost everywhere east of the Rocky mountains in the United States and Canada. Specimens from Louisiana, Manitoba, and Virginia do not vary appreciably. The larvae inhabit very moist soil and soil temperature cannot be of any magnitude. The habitat and larval habits are such that variations due to differences in temperature and moisture are not common. If the soil becomes too dry the larvae leave it and dig a new burrow in soil of the wetness required by the species. Since they occur near water courses, this tends to keep larvae in similar conditions no matter in what latitude they occur. The variation of *oregona*, a related species, has not been studied.

*C. hirticollis* occurs on the sandy shores of the sea, lakes, and rivers from Vera Cruz to California, the Great Lakes, and Massachusetts. The pattern which is shown in figure 330, plate XVI, is quite invariable as compared with the rest of the species considered. High temperature experiments performed with these showed clearly recognizable modification in which the pattern duplicated Southern and Southwestern forms. The experiments and geographic and other variation are likewise parallel.

*C. sexguttata* has been studied and shows peculiar variations. Specimens from the Northeastern United States and the region of the Great Lakes have well developed markings (Figs. 525 and 526, Pl. XXVIII).

The same is true of Texas specimens. Specimens from E. Tennessee are reduced as in figure 523 and those from eastern Kansas are usually immaculate with a few like 523.

*C. punctulata* representing the Mexican group, has been studied and while widely distributed fails to show pattern varieties and did not show any modification when subjected to 40°C in the experiments. It also shows no geographic variation in markings. *C. lemniscata* shows the vitta broken in about seventeen out of seven hundred and fifty individuals. These patterns are like *luteolineata* (Fig. 24, Pl. III). *C. carthagena*, *haemorrhagica* and *C. gabbi* of San Diego, California, show a tendency for the markings to disappear by the spreading of pigment over the areas of the markings.

## COLORS OF TIGER BEETLES

### CAUSES OF COLORS

The pigment present in the cuticula of *Cicindela* is essentially all in the primary cuticula (Fig. 1). This pigment has been demonstrated by Gortner to be melanin and not the compounds stated by Tower (1906). This pigment is, in all the elytra observed, either brown or black. It is the result of the oxidation of tyrosin or related compound by tyrosinase (Riddle, 1909). In the case of all elytra examined in transmitted light which covers nearly two hundred species no color but dark brown ranging to black has been observed, no matter what brilliant spectrum colors were present in the elytra as view in reflected light.

Professor Michelson has made a study of the causes of the bright metallic and spectrum colors in various insects and feathers and has found that the colors are due to very thin surface films, metallic in character. He has very kindly examined elytra of several species, including *Cicindela chinensis* Dej., several varieties of *C. limbalis*, and several color varieties of *C. scutellaris*. The colors of the first two differ in different parts of the same elytron, the second named species showing blue and red and differing sometimes in the same population from black to green or blue, red, etc. The first two species gave results too indefinite to report. The third species, *C. scutellaris*, occurs on the Atlantic coast as a brilliant green form with some dead black forms among them in the same population; and in Kansas and Oklahoma the population is a flame red. The red *scutellaris* from Kansas showed a "preponderance of red in the spectrum, negative phase change at red end of spectrum, and positive phase change at blue end. The green, east-coast forms showed excess of blue-green with positive phase change at red end and negative phase change at blue end." The black form which occurs as a part of the general population with the green is

without trace of color and acts like a piece of black paper. They are merely without the film over the surface.

Professor Michelson states further that the colors are chiefly if not entirely true surface or metallic colors. They are produced by a film of ultra microscopic thickness probably less than a ten-thousandth of a millimeter. He is inclined to attribute differences in the colors to differences in the chemical constitution of the film and color changes during ontogeny to changes in chemical constitution, but states that this would be very difficult to demonstrate on account of the minuteness of the film. The work of Heylaerts (1870) (see page 48) would seem to indicate that physical conditions or differences cause a change or difference in color in dried specimens.

Tower's figure copied by Folsom must be incorrect as he shows such a film as seen under the microscope. This line which he draws appears as a dark line under the oil immersion lens; it is probably a total reflection line which he misinterpreted under the influence of Professor Michelson's verbal statement, that surface films must be responsible for brilliant colors, which preceded the latter's investigation by several years.

The colors of the group which are on the whole exceptionally brilliant are to be attributed to a brown or black pigment either without or with any film or with films of varying effectiveness and with varying effects on the light reflected from the surface. A change in color with a change in the angle of incidence indicates the presence of metallic film.

#### ONTOGENY OF COLOR

One of the striking phenomena in connection with the study of the ontogeny of patterns is the ontogeny of color as opposed to pigment. Plates XXIX, XXX, and XXXI are devoted to this subject and show a series of radical changes in the character of the coloration associated with stages of development. Plate XXIX is devoted to the ontogeny of color in *C. scutellaris lecontei*. Figure 543 shows the beginning of color on the ventral side which consists of bluish reflections, at first about the center of segments which later become green. Later figure 541 shows purple reflections at points which remain so throughout without change, showing that changes do not always take place. The tip of the abdomen and trochanters appears not to have a surface film.

Considering the colors of the dorsal side and elytra we note that at the beginning the color is a yellow, the usual color of the cuticula when backed up by the tissues, with greenish reflections. After a little time green color begins to appear more prominent and the elytron of



this normally brown species resembles the green form of the Atlantic coast (Fig. 553), differing only in lacking bluish reflection. From 3 to 15 days yellow reflections are at their maximum. Specimens occasionally are collected in this stage (September). After this the color begins to shift to red or dull brownish red, but has still greenish reflections in some individuals which gradually disappear with hibernation. The reddish reflections lose luster and turn to a dull brown by the time the adult dies in the latter part of June after reproducing (Fig. 551). Important differences occur between individuals collected at different times of year.

Figures 559 to 562, plate XXX, show the development of the color in *C. hirticollis*. Here again the color begins as green and gradually shifts to brown or reddish brown. There are no green varieties of this species but it often shows greenish reflections in the adult condition. This is more pronounced in fresh individuals.

Figures 563 to 565 show the development of the color in *C. purpurea*; the first stage shown (Fig. 563) compares favorably with some forms of the variety *graminea*. As time goes on the color shifts to red over the upper surface of the elytron and the blue margin shifts to green, both shifts being down the spectrum. Black specimens occur with this species in the locality where the larval stages were collected for these observations.

*C. purpurea limbalis* shows a similar series of stages, and the shiftings which are similar to those in the form *purpurea-graminea-auduboni* shown above. In general during ontogeny in the species noted the color shifts down the spectrum as the cuticula hardens and pigment appears. In fact from blue to green the change is direct; but in passing from green to red the orange and yellow are not noticeable or at most occur as slight reflections; green changes to reddish green, red, and finally a dingy brown almost black in a few individuals collected in August and September with the new generation. A series of individuals killed, pinned, and dried so as to show a series from the beginning of color development to completion, is remarkable in that the earliest stage when dried is dull black, the second purple, the third blue, and individuals in the green stage (Fig. 573, Pl. XXXI) usually turn fiery red on drying (Fig. 576, Pl. XXXI). Heylaerts (1870) performed experiments on color changes in some European species. Brown specimens of *C. hybrida* when heated to 102°C. turn green and remain so for a short time when exposed to the atmosphere. The change to brown is hastened by blowing the breath on them. They remain green in a sulphuric acid desiccator. Green *C. campestris* turn blue when similarly treated. These changes accompany the almost complete removal

of moisture from the surface film and are in the opposite direction as compared with the ontogeny changes and the changes which take place on drying of fresh immature specimens. The cause of these physical changes is unknown. Other shiftings in color have been noted; one of these in *C. lepida* is of particular interest as the change is in the direction opposite to that already noted. *C. lepida* has the elytron nearly all white but such parts as are pigmented are green in the adult. When the pigment begins to develop it is a brilliant gold and remains so for several days, finally changing to a dark green. In this case the change is the only one of the kind noted. Golden yellow blending with green is commonest in *cuprascens sperata*, *circumpicta*, and related species. These may shift from green to brown through yellow instead of red but their ontogeny has not been studied.

Even the dull species like *C. 12 guttata*, and *repanda*, and occasionally *C. punctulata* show more green in the early stages and turn brown as they mature. The early stages of *C. tranquebarica* are blackish green, gradually turning bronze brown as more pigment is developed. *C. formosa* is at first reddish and gradually changes to brown; some individuals collected in the autumn are red.

#### RELATION OF ONTOGENETIC STAGES TO GEOGRAPHIC RACES

First of all it should be noted that there appears to be no good reason for assuming that the biogentic law holds good with reference to these color changes; it would be only the most radical adherent who could see it applying. However in a general way the developmental stages of a given species, like *C. scutellaris lecontei*, may practically reproduce the color of another variety in ontogeny. Compare figure 546 with figure 553, plate XXIX. The stages in the development of typical *C. purpurea* do quite exactly duplicate some of the races recognized. Thus the stage shown in Figure 563 practically duplicates the color of *graminea* while Figure 564 duplicates some of the specimens of the subspecies *10 notatta*.

Again in Figure 572 appears an ontogeny stage which resembles very closely the variety *denverensis* but is less yellowish; *denverensis* also usually lacks the blue green margins, though the green is purer and brighter along the margin, showing a difference comparable to that seen in nearly all specimens of *purpurea*.

*C. hirticollis* shows a stage in the development of color (Figs. 559 to 562, Pl. XXX) which corresponds very closely to the race of the species occurring on the Pacific Coast. In addition to this it shows slight reflections of the bluish of the bluish drab forms of Vera Cruz. Reddish brown forms occur in southwestern Kansas.

Occasional specimens of *C. tranquebarica* collected in Massachu-

setts, show the dull green occurring in ontogeny. Similar greenish reflections occur in the western forms, but this blends with dark color instead of brown.

The light wine color of the high altitude form of *C. formosa* (Salida, Colorado, 7000 ft.) is duplicated in the ontogeny of color in *C. formosa* from near Chicago. Specimens which have this color are sometimes collected in the late summer near Chicago, but none have been taken in the spring.

*C. punctulata* appears not to possess a film such as described, as a rule, and the changes during ontogeny are not marked. The brilliant green forms which occur in the southwest have no counterpart in ontogeny.

Nearly all the species of the *tranquebarica* group, as well as many others, show a great series of colors. The following shown in Table II occur:

TABLE II  
Showing Colors Occurring in Several North American Species

	Black	(Blend)	Brown	(Wine)	Red	(Blend)	Green	(Blend)	Blue	(Blend)	Violet	Orange	Yellow
<i>scutellaris</i> .....	x		x	x	x*	x	x	x	x		x	*	
<i>purpurea</i> .....	x		x	x	x	x	x	x	x				
<i>sexguttata</i> .....	x						x	x	x		x		
<i>tranquebarica</i> .....	x	x	x	x		x	x	x	x				
<i>nigrocoerulea</i> .....							x	x	x				
<i>oregona</i> .....			x	x**			x	x	x				
<i>formosa</i> .....			x	x	x								
<i>hirticollis</i> .....			x		v		x		x***				
<i>repanda</i> .....			x		v		x						
<i>willistoni</i> .....			x		v		x						
<i>fulgida</i> .....			x	x	x								
<i>pulchra</i> .....				x									
<i>anthracina</i> .....	x						x	x	x				
<i>pimeriana</i> .....							x	x	x		x		
<i>cuprascens</i> .....			x	x			x	x				x	
<i>lepida</i> .....							x	x				x	x

\*Reflections in western forms.

\*\*Reddish brown.

\*\*\*Dull bluish drab. Vera Cruz, Mexico.

In *scutellaris*, *purpurea*, *anthracina*, and *sexguttata* black and green forms are mixed, i.e., the species are dimorphic. The same is probably true of *tranquebarica*, as *plutonica* appears to be rare and

occurs in California where the usual population is green. The physiological condition in which no metallic film is secreted is closely related to one in which a metallic film producing green is secreted.

The secretion of a film which lies at the outside of the primary cuticula is the first work of the hypodermal cells. It would seem that the secretion of such a layer might be inhibited by environic stimuli at a critical stage in the life of the pupa, but there appears to be no experimental results showing whether or not this is true. If environmental conditions do influence the occurrence of black and green, climatic conditions applicable to all species are not alike (see p. 52).

In the case of *C. scutellaris* the green and black forms have least pigment developed in the elytra (black is accompanied by a similar amount), and green in ontogeny is accompanied by least. The amount increases as the reddish color comes in, in *lecontei*. The amount of pigment in the brilliant red western form is intermediate between the green form and the dark red *lecontei*. *C. splendida*, very brilliant, shows much less pigment than *limbalis*, which is dull.

Many species, particularly *purpurea* and *pulchra*, show more brilliant colors along the elytra margin where white markings usually occur. This is noticeably true in *purpurea*, which in the subspecies *cimarrona* has a complete white margin in many specimens. As a rule when the areas commonly occupied by markings become pigmented the colors in these areas are more brilliant. W. Horn (1915) has called attention to this. As has been noted, the elytral surface of most tiger beetles is made up of small hexagonal pits which probably correspond to the hypodermal cells which secreted it (Fig. 1, Pl. I). The ridges between these lie over the boundaries of the cells. In the elytra of *C. purpurea* these pits are smaller in the blue-green margin. The same is true of many other species as shown in Table III.

While many colors such as green and greenish blue, red, etc., in early ontogeny change to colors of longer wave length during ontogeny and later life, such is not true during ontogeny at least in the case of such purple specimens of *C. scutellaris*. These are rare and only a few specimens from Starved Rock (Utica), Illinois, have been found; some of these are purplish brown, but one individual was secured in the larval stage and reared (Fig. 558, Pl. XXIX). It was purple from the beginning and never showed any tendency to change, though it was kept for a long time. The same is probably true of the purple forms of *C. sexguttata* which occur in eastern Kansas; purple forms of *nigrocoerulea* show no blends with the green.

TABLE III

The following table shows the relative size of hexagonal cups in various forms and parts of the same clytron, etc.

Species	Variety	Locality	Organ	Part	Color	Diameter in mm.
<i>C. purpurea</i> .....	.....	Massachusetts.....	clytron	margin	green.....	0.0115
" "	.....	Chicago.....	"	disc	red.....	0.0150
" "	.....	"	"	margin	green.....	0.0115
" "	<i>denverensis</i> .....	Denver.....	"	disc	".....	0.015
" <i>scutellaris</i> .....	<i>lecontei</i> .....	Chicago.....	"	"	brown.....	0.0150
" "	<i>scutellaris</i> .....	.....	"	"	{ red.....	0.0150
" "	<i>scutellaris</i> .....	.....	"	"	{ ".....	0.013
" "	<i>scutellaris</i> .....	.....	"	"	{ green.....	0.0115
" "	<i>rugifrons</i> .....	.....	"	"	green.....	0.0100
" "	<i>modesta</i> .....	.....	"	"	black.....	0.0100
" <i>generosa</i> .....	.....	Colorado.....	"	"	red.....	0.0150
" <i>chinensis</i> .....	.....	China.....	"	disc	{ blue.....	{ 0.015 to
					{ metallic.....	{ 0.0225
						{ 0.018 av.
						{ 0.013

## GEOGRAPHIC VARIATION IN COLOR

The black forms of *C. scutellaris* are found to occur in some New York localities, and some New England localities, but are less numerous than green ones. A complete catch from Providence, Rhode Island, for one season, including hibernated and freshly emerged forms, showed less than 20 per cent black individuals; a similar catch from Framingham, Massachusetts, gave no black individuals; 112 specimens from Aqueduct, New York, showed about 15 per cent black. Some localities in New Jersey show, according to Leng, a majority of black forms in spring. A small catch from Baltimore, Maryland, showed more than half black forms. At Raleigh, North Carolina, black forms do not occur, and I find no records for Virginia, North Carolina, and South Carolina; but black forms occur in Alabama, Georgia, and Florida. At Mobile a few black ones are found in the autumn but very few or none at all in the spring, according to Messrs. Loding and Van Aller who have been interested in them for several years. None are recorded for points farther west.

Black forms of *C. sexguttata* likewise occur in the eastern states, New Jersey and Pennsylvania, but not in the southern localities. Black forms of *C. purpurea* (see map, Fig. 472) occur in Illinois, Iowa

Minnesota, Kansas, Nebraska, South Dakota, Colorado, Utah, Wyoming, and New Mexico, but are very rare in eastern localities. Mr. C. A. Frost secured one bluish black individual in Massachusetts. The black forms of *C. tranquebarica* are recorded from a single locality in California. No black forms occur in the localities where black forms of other species occur though blackish green forms occur in the Pacific States and blackish brown, in the Gulf States. Likewise there is no correlation between geographic conditions and green forms. *Scutellaris* is green on the Atlantic coast, *purpurea* in the central and northern great plains, *tranquebarica* on the coasts and coastal mountains.

Exclusive of black forms which have just been discussed the geographic variation of colors in the species belonging to the *tranquebarica* group, may be stated as follows: Geographic variations in color are of special interest in the case of *C. scutellaris*; I note green forms predominating in all specimens in the Atlantic Coast and Gulf States. Bluish reflections characterize these as a rule, particularly in some localities where occasional blue forms occur (Fig. 470 a).

In Texas along the northeastern border near Oklahoma forms occur with a decided golden cast which in series in some localities range from bluish green through green with golden cast to flame red like figure 554, plate XXIX; north of this flame red predominates. Forms with flame red elytra and green or blue thorax occur west to the Rio Grande, occupying a triangular area with its apex just north of the Black Hills and eastern point near Topeka, Kansas. Points a short distance west of the Missouri River such as Topeka, Kansas, and Superior, Nebraska, show great variation in marking and all intermediate color conditions between the forms with flame red elytra and those of the dull brown and wine color occurring to the east and north of the Missouri River. The most brilliant wine colors occur between the Mississippi and Missouri Rivers and in Manitoba; near Chicago the brilliant wine colors are not usual, but greenish browns and greenish individuals are common. There appears to be no close correlation between the distribution of these colors and any mapped distribution of factors.

*C. purpurea* is very variable; figures 471 a, 472 show color varieties of this species. In general among the groups in which the markings are withdrawn from the margin, the forms with the upper part of the elytron reddish and its margins green are most widely distributed, extending almost throughout the range of the species except the Pacific coast specimens which are golden green (Puget Sound, 10 ft.). The eastern forms are of the typical red elytroned type. In the entire Mississippi Basin, Great Plains, and Salt Lake Valley this is mixed with green and black forms, the latter two predominating in the west-

ern Great Plains. In the New Mexico localities dark brown forms (*cimarrona*) occur. There is no correlation between color and mapped climatic conditions unless it be rainfall.

Considering the *purpureas* in which the reduction of markings leaves only a small dash at the margin of the elytron, one notes that the wine colored specimens are distributed throughout the region of the Great Lakes and in Manitoba and generally westward to the Missouri River, and Colorado. This type is distributed in a general way north of about 41 degrees North Latitude and has the thorax the same color as the elytron. The forms *splendida* and *transversa* are similar in color but have the thorax green or blue and the elytron either red or wine color, they are distributed south of the form with red thorax and in the eastern part of the range are less brilliant than farther west. The more western forms have brilliant red elytra similar in color to that of the red *scutellaris*. Mixed with these are the green forms; in western Kansas and Colorado, especially, they occur with the red forms and are often taken in coitus with them. The green form is evidently merely a color aberration of the red form.

The color variation of *C. tranquebarica* is not striking over the entire area east of the Rockies. Nearly all are simply dull brown. Specimens from the moist southern states are usually duller blackish brown than the northern forms. No striking color varieties occur even east of the Pacific states and Idaho. In some parts of eastern California (Bridgeport) they are brown, while only a little way west they are green; further surprising differences were found in Nevada. At Caliente the writer took brown *tranquebarica* and blue *oregona*, while at Las Vegas he took green and bluish *tranquebarica* and no *oregona* which occur there and are probably green also, but there is no apparent reason why *oregona* should be blue or green and *tranquebarica* brown in a region where both are likely to be green.

*C. generosa* is brown and wine color in eastern localities and where *purpurea* is similarly colored. Near Chicago the colors are similar. At Topeka, Kansas, the color varies considerably, reddish, bluish, and greenish brown occur. South, and southwest from this point the specimens are progressively redder. The most brilliant forms are the red ones from western Oklahoma, western Texas, and Colorado. At low altitudes these are golden red. Wine red occurs at high altitude (Salida, Colorado, 7,000 ft.). *C. hirticollis* has already been discussed (see page 49). With the exception noted there is little variation and distribution is transcontinental and from the Great Lakes to Vera Cruz.

## EXPERIMENTAL MODIFICATION OF COLOR

This is fraught by many difficulties on account of the remarkable series of colors and color changes occurring in ontogeny, and the usual early death of individuals reared under experimental conditions. Figure 555, plate XXIX, shows an experimentally modified individual of *C. lecontei*. The presence of the yellowish color in the markings indicates that secondary cuticula has been secreted with the air spaces between, in quantity sufficient to give the opaque appearance to the markings. This specimen in particular was known to have died 15 days after it was dug out of the soil, which is not until the cuticula is well hardened. Its markings are reduced below anything ever found near Chicago. The color shows an unusual amount of yellow and approaches most nearly to some of the western forms of *scutellaris* (Fig. 554) though not exactly like any forms known to occur. This particular individual showed more yellow and was most generally modified, leaving no doubt as to the fact that color modification had occurred. Three other individuals, all of which lived long enough to show the development of opaqueness in the white markings, were produced and showed green of unusual clearness from reddish brown and suggestive of green forms rather than the parent stock of *lecontei*. All these were in dry conditions. The warm moist experiments showed green forms but not clearly differentiated from ontogeny stages in part due to early death.

Three specimens (Fig. 557) were brought through successfully in icing experiments and lived two weeks or more. Two of these were characterized by broad markings and dull brown elytra and rather striking differences between the color of the head and the thorax, the latter being quite green. Figure 557 shows considerable modification of form and size not noted in the other two. The very rounded ends of the elytra, and square shouldered character was quite striking and in direct opposition to the usual tendency shown in the rest of the group.

Figure 556 shows a specimen brought through at 37°C. with marked acceleration of development. This individual was small, slender in the head and thoracic region, with the elytron widest in the region behind the middle band. The color is much brighter and freer from dull brown reflections than that of the normal specimens, having a decided brilliancy to the color. This specimen was kept alive until the opaque appearance of the markings was well developed. This body form is characteristic of many specimens from the extreme southern states. There is a noticeable general tendency toward this general body form in all individuals reared in high temperature.



Experiments were performed on *C. hirticollis* which paralleled those noted on *C. scutellaris*, but with results on markings and none so far as color is concerned. It is probable that the experimental individuals showed more green than others, but the difference is too slight to justify an unqualified statement to that effect. One striking result was obtained in the experiments where the temperature of about 37°C. was maintained on larvae which had not hibernated; one small individual was obtained (Fig. 566) which however retained all the striking characteristics of the species.

Experiments on *C. tranquebarica* were successful. Specimens reared in temperature of 37°C. and much moisture (Fig. 570) showed the dull blackish brown which characterizes the colors of some of the specimens from the moist southern states. This color was not uniform throughout the series so raised, but was much commoner than in the case of specimens reared in hot dry conditions, as these are more brilliant (Fig. 569). A number of specimens were iced but only one of these was especially peculiar (Fig. 568). This was decidedly *more red* than any others seen in the course of my studies. Some of the iced specimens were unusually dull, however, and no uniform results were noted except that the heads were uniformly greener.

*C. limbalis* was subjected to high temperature. In the moist conditions dull colors were obtained. Figure 577 shows one of the high temperature individuals in which the color is deeper red and the reflections more striking blue than in the normal specimen at this stage (Fig. 575). 579 which shows an individual subject to high temperature in moist conditions is more generally dull green. 578 shows an iced specimen which is similar to the warm moist individual. These differences are slight and not very convincing, but the individuals are different from any reared or collected under other conditions.

Experiments of a similar character were performed on *C. punctulata* but appeared to be without results. A similar series on *C. lepida* were likewise without results.

#### RELATION OF COLORS AND COLOR PATTERNS TO CLIMATE

After a thorough study of the subject and comparison of the distribution maps of several species with maps showing the rate of evaporation of water for the year, the evaporation of water from the porous cup atmometer from April to September, the ratio of rainfall to evaporation, mean annual temperature, temperature April to September, and with maps showing cloudiness, humidity, rainfall, etc., it was demonstrated that the distribution of color varieties, and pattern varieties even where the types are quite distinct, is not correlated with the conditions shown on such maps.

In general such correlation is closest in relation to rainfall, but this correlation is not so good as one would expect (Fig. 470 *a*, Pl. XXIV). This is perhaps to be expected in the case of species which belong to local conditions which is true of most of the species of *Cicindela*. This subject has been discussed in some detail (Shelford, 1911). Here it was shown that species which were distributed in a major climatic habitat had a distribution correlated with the distribution of vegetation, which in turn is correlated with the distribution of climatic conditions. I showed further that species such as *C. tranquebarica* traversed almost the entire continent without much variation by virtue of living in moist soil, due either to climatic moisture or to local stream moisture or lake-shore moisture. *C. scutellaris*, *C. purpurea* and most of the other species noted are found in some special kind of soil such as sand containing a little humus (Shelford, 1911, 1913b) or steep clay banks or some other restricted situation. Taking *C. scutellaris* for example, this species being found in well drained or dry sand containing a little humus and bound by scattered vegetation throughout its range, it is to be expected that the distribution of the species will be correlated with some sort of measured soil conditions such as soil temperature, soil wilting coefficient, or the like; but no such conditions have been recorded or mapped. There is some evidence of soil effects in this species (see Fig. 558, Pl. XXIX). Some specimens from the very coarse sands resulting from the weathering of St. Peter's sand stone, near Utica (Starved Rock), Illinois, are purple. No purple forms have been taken elsewhere. Two specimens from sandy clay (Suman, Indiana) had an unusual silky appearance. When soil temperature work under way is published, I shall attempt to make use of the extensive records which have been accumulated for the purpose of working out correlation between conditions and color and pattern varieties. Conditions associated with altitude influence color in some cases, but there is no unity of conditions or colors.

#### GEOGRAPHIC CENTER OF THE GROUP ON THE BASIS OF PATTERNS

The usual criteria for the center of distribution (Adams, 1902) indicate that the Oriental region or at most the Oriental and Ethiopian regions (shores of the Indian Ocean) are the geographic center or center of distribution of the group. The first evidence presented which indicates this is found in table I, in which eleven groups of species are shown to occur in the Oriental region and in other regions, while not more than six occur in any one other region and at the same time in still others.

Patterns are divisible into three great groups: first those without the spots at the base and along the inner border of the elytron shown to the left of the bottom of figure 580; these patterns represent the

usual type of the group and are world wide in distribution. The patterns to the right of these are those with the basal spot and the two spots along the inner border, shown on the map by the stippled area; this includes a number of pilosity groups and thus represents considerable diversity. The group in which the middle cross band (4) is oblique in the reverse direction as compared with that which is usual in the group as a whole, is shown by small circles. This is essentially confined to the Oriental region. There are a few species in Africa which show this and which appear somewhat related on the basis of pilosity, but circles are omitted. The group of species and patterns shown at the extreme right and represented on the map by the short oblique lines constitute a group divided between the Oriental and Australian regions.

An over-lapping of the various types in the Oriental region is evident. This would place the center for the group in that region but several African species appear to be most primitive from the standpoint of kind of patterns shown. It accordingly seems best to consider that the lands adjoining the Indian Ocean constitute the center of distribution of the group.

### GENERAL DISCUSSION

The evidence which must support any conclusions drawn is of such a character and drawn from so many sources that the presentation of a few lines of evidence and the conclusions forthcoming from them can best follow the general presentation of data and minor conclusions on the preceding pages. Since color and color pattern are quite distinct so far as laws governing them are concerned, the discussion of the two will be separated.

#### PATTERN TENDENCIES

Under this head we are concerned with (a) the original type, (b) the most characteristic elements and combination of original characters, (c) general laws of pattern modification applicable to groups of species, (d) laws applicable to particular species, and (e) laws applicable to subdivisions of species.

As has been noted the number of directions in which modification has preceded are numerous and any statement of such directions is difficult and has led other authors to make general statements regarding the modification of patterns which were general enough to apply to a large number of species.

The earliest account of variation in the color, or markings or the patterns of tiger beetles is that of Dr. Geo. H. Horn (1892). He took

the markings of *C. tranquebarica* Herbst as the underlying type "from which all forms observed in our Cicindelas have been derived". He bases this statement on the fact that it is the so-called humeral lunule, middle band, and apical lunule which give similarity to the patterns of the genus. He states that modification occurs in any one of four ways:

- A. By progressive spreading of the white.
- B. By gradual thinning or absorption of the white.
- C. By fragmentation of the markings.
- D. By linear supplementary extension of the white.

These tendencies are all recognizable, all of them occurring in the course of individual and geographic variation of single variable species.

Walther Horn (1908) in *Genera Insectorum* discussed the patterns from a somewhat different point of view. He states that in the ideal sense the markings which he recognizes as the humeral, apical, and middle spots are made up of 3 humeral, 4 middle and 3 apical spots as shown in figure 290, plate XV, and 333, plate XVI. Thus he calls the markings which are most characteristic of the group the *Marginal Component*. He calls the median basal spot of the elytron the *Basal Component (B1)* and the marking along the suture or anal border of the elytron the *Sutural Component*. He recognizes also such patterns as those shown in figures 241, 243, 248, as *Dispersion Component*. He states that this analysis is for taxonomic purposes only and not based on ontogeny. He recognizes the most important tendencies toward joining of spots, in addition to the general plan outlined in G. Horn's four statements.

The work of these men is here cited to show the fact that various generalizations have already been made showing that the patterns conform to a general plan of spots or bands which have been similarly interpreted, though not exactly the same, by two authors with wide experience in the group.

For the purposes of illustrating what may be determined in the group in the way of general tendencies (p. 36) and the patterns of *interrupta*, *interrupta* subsp. *gabonica*, *flexuosa* (Pl. XII), *tranquebarica*, and *purpurea*. And for a second illustration take the same species substituting *scutellaris* for *purpurea*.

First noting *interrupta* and *gabonica*, (Figs. 156, 156 *a* and 165, and 165 *a*) one finds that the cross bands clearly recognized in Coleoptera, especially *Chrysomelidae*, and *Lepidoptera*, and which appear in the tiger beetle group especially in the patterns associated with *interrupta* (Pl. XII), and which appear in all the species in which ontogeny was studied, are present. In *gabonica* it appears that through individ-

ual variation the characteristic joining to make the "middle band" is indicated. This occurrence of cross bands as noted and the variations of *interrupta* together with the light stripe in the region of joining of the cross band 4 with cross band 5.6 which occurs in the ontogeny of the patterns of *scutellaris* constitute the evidence for the line of development suggested.

The *second tendency* to be noted is the shifting of the spots near the sutural or anal border of the elytron out of line with the cross band with which are properly associated. This is shown in figures 156 and 156 *a*, plate XII, *interrupta* and in figures 153 and 154 in *flexuosa*.

The *third tendency* to be noted is the loss of the three small basosutural spots (*B1*, *C2.3*, *D4*, Fig. 49, Pl. V). This usually takes place in a definite order if individual variation may be trusted as an indicator. At least these may have disappeared in some definite order leaving the typical pattern of *tranquebarica* as shown in the controls of the experiments (Figs 456*a'*, *b'* and 457 *a'*, *b'*). This type is shown in figures 31, 32, and 33, plate III, and the elements from which it is made are shown with others in figure 49, plate V. As further evidence of the longer persistence of *C3.4* see figure 125, plate X, and figure 145, plate XI, which are late stages showing the persistence of this spot after the more anterior one has disappeared.

The *fourth tendency* which may be noted is the tendency for the typical *C. tranquebarica* pattern to shift as indicated in the patterns which result from experimental stimulation during ontogeny. This is shown in figures 456 *a*, *b*, 457 *a*, *b*, 458, 459, and 460 *a*, *b*, plate XXVIII. These modifications have already been noted on page 39 but may be recalled briefly as follows: the forward and backward extensions of the inner end of the humeral lunule (spot *B2* drops out) disappear; the slight forward extension of the inner end of the middle band in the longitudinal stripe *C* (*C5*) drops out or loses identity. The withdrawal of the middle band from the elytral margin and reduction to conform with that of *C. purpurea* (*purpurea*) (Fig. 537, Pl. XXVIII) is the striking and probably the most important change best illustrated in 460 *a*, *b*. Similar modifications in all high temperature experiments with *C. hirticollis* (some with *C. limbalis*) serve to clinch the argument for response in definite directions.

A *fifth tendency* is illustrated by *C. purpurea* as shown in the figures to the left in figure 537, plate XXVIII. The differences between the *purpurea* series and the *tranquebarica* series lies in the short humeral lunule of the former, which indicates a different tendency which perhaps constituted the original distinction between the patterns of the two series.

Turning to the *scutellaris* series one notes that markings are reduced by high temperature (Figs. 463 *a, b*, -, 464 *a, b*, -, Pl. XX). The original markings evidently included a middle band like *purpurea* (Fig. 512, Pl. XXVIII). As evidence for this note figure 490, plate XXVIII, which shows a reduced band present, and figure 115, plate IX, which shows one in ontogeny which does not persist in the adult at all in individuals from the central states. Stimulation of *scutellaris* during ontogeny by high temperature merely reduces the markings concentricly, withdrawing the middle band from the margin as well as from the centre. This is the type of modification which has led to immaculate forms in the south and southwest.

Cold extended the same markings, but the results are not so striking in general plan though perhaps equally general in application, as markings are lost in the same general order in many species if individual and geographic variation may be used as an indicator. First we have noted that *purpurea* is divided into two groups, one the steep-bank-inhabiting group and the other the level-ground-inhabitant. The latter (Pl. XXV, left, and Pl. XXVIII, Fig. 537) loses its markings in the manner suggested above, as indicated by the experimental results with *C. tranquebarica*. The outer end of the band being lost first. The other loses its markings as does *C. scutellaris*. Compare 486 to 490 with 506 to 510 and 522 to 525, plate XXVIII, which indicate the loss of markings of several species along similar lines, i.e., through retreat to the margin and then reduction of the marginal markings. Thus the response to high temperature represents a tendency present in many species.

The large confluent markings of Manitoba specimens and of those which have been subjected to cold suggest that a second type of response may be in the form of a concentric extension of the unpigmented areas. It seems evident that the mechanism in *C. scutellaris* may be thrown in either direction from the general average of the species.

I have followed through a series of marking modifications and shown evidence for the tendencies indicated. It would be futile to present further discussions of a similar type regarding other species, as particular weight is given to experimental results and such results are wanting in other species. The reader by an inspection of the figures which are particularly numerous and selected for the purpose will note that in many groups one species begins in pattern modification where another leaves off. This fact was noted by G. Horn (1892). In many cases an exact knowledge of the geographic variation of the species is not available, but figures 435 to 437, plate XVIII, show a series which is supported geographically. *C. curvata* which occurs in Mexico

is first in the series, *dorsalis saulcyi* which occurs in Texas next, and *dorsalis* which occurs in New York and New England shows spreading of the white. This series is representative of one in which the patterns are of a specialized type, in which the media trachea is reduced. Forward curves in the humeral lunule are very rare; one specimen of *saulcyi* in the collection of Mr. Gestro in Genoa has this marking curved forward. The backward curvature occurs also in *trifasciata peruviana* but is rare. Figure 434, plate XVIII is probably this species.

Much detailed study and collecting is necessary to show that the differences which enable one to arrange a group of patterns in series really represent a series geographically or habitually separated, and the writer refrains from further discussion of such cases though others might be cited with little doubt as to their validity. The patterns in the illustration pages are arranged to show probable lines of modification. The large series of parallel trends shown in different groups leaves little doubt that the tendencies shown are highly probable.

Another tendency quite common in the Cicindelas is the degeneration of the media trachea. The shifting of the pattern in that region is one of the first modifications to take place if we may judge from the existing patterns and from individual variation. The complete breaking up of the system of markings appears first in this part of the elytron. This degeneration of the old system of markings has proceeded far in some species such as figure 16, *nivea* and figure 21, *tenuipes*. Here an almost entirely new system has grown up, but derived from the older one. These cases constitute our best evidence that these patterns are highly specialized. The morphological structures with which the pattern is associated, are modified; some of the important parts have degenerated.

In considering these patterns and the modifications which take place the reader must not fail to note that there are physiological problems to be considered and physiological work to be done. The explanation for the occurrence of pigment in some parts of the body and not in others may be very simple. In course of experiments concerned with the production of abnormalities, it was found that the labrum which is not pigmented in the species used, develops pigment in the area of wounds. Specimens with abnormal elytra which appear to be due to injury or irritation nearly always have reduced patterns, but no cases in which the white markings are extended are recorded. Thus it appears that the present adult areas of pigmentation and areas of ontogenetic and earlier pigmentation may be merely areas occupied by cells with a higher rate of metabolism. This in the normal elytron

may be due to advantageous nutrition conditions arising from the morphology of the wing, or to special characteristics of the cells themselves.

#### BEARING OF THE COLOR PATTERN MECHANISM ON ORTHOGENESIS

Orthogenesis is commonly understood as evolution in certain direction as opposed to evolution due to the survival of certain kinds of variations out of a large fortuitous series. The chief points in the original contention of Eimer, namely, that progress in species formation has been along definite lines, has been so generally admitted that the remaining matters are concerned with such questions as: How definite have the directions of modification been? What are the causes of certain directions of modification being developed to the exclusion of others? Are the causes external or internal? Whitman has emphasized the internal causes, which is the tendency of all who come at the problem from the point of view of embryology, cytology, and modern genetics. The mystical nature of the question of the origin of a complex organism from a single cell, transmitted through the egg and the sperm of the entire series of details which are inherited, have fascinated men and led to the general acceptance of theories which involve the insulation of the bearers of hereditary characters from the environment. The evidence at hand does not justify any detailed discussion of this problem but I will turn to the few things which appear to apply to the tiger beetle group.

The effects of high temperature on *tranquebarica* produce variations in the direction of shortening the longitudinal portion of the middle band and throwing this marking into an oblique position. This is also one of the general tendencies in a large group of tiger beetles. In *tranquebarica* it occurs as a response to stimulation, and in its races of unknown stability in regions in which high soil temperatures may be expected. It occurs in nearly half the species of the group of tiger beetles as a regular, probably hereditary character. The condition of the middle band seems to be due to a mechanism of response or modification, which is the same in these responses to stimuli and in the regular heredity trends. The problems of heredity then appear to be the same as the problems of development and modification of this elytral character of *Cicindela*. Perhaps the weakest point in the entire method of study and reasoning of those interested in problems of heredity is the apparent practical assumption that laws of heredity are not the same as laws governing characters, in particular organs, and as laws of response. The evidence presented tends to show that these laws are one and the same and are dependent upon a mechanism present in the elytra of many species of *Cicindela*. If this is what is



meant by orthogenesis this group illustrates the orthogenetic principle.

The illustration above is concerned, however, with only one of several kinds of tendencies which appear in the group. Still another principle is suggested by the experiments. If extension of the unpigmented areas is indicated by the experiments with cold conditions during ontogeny, which would be supported by geographic variation in many species, one is forced to the conclusion that different kinds of stimuli acting on the pattern mechanism produce different responses. One type of response is the extension of the unpigmented areas. From an inspection of the figures it appears that this may take place on the basis of a pattern in any stage of reduction. As a rule it occurs in correlation with some marked change in the basal structures of the elytron at least when the extensions violate the original plan of the pattern. The mechanisms of pattern heredity and pattern development possess the capacity both to respond to stimuli by changes in form and by the extension of the unpigmented areas. This extension of the unpigmented areas may take place in almost any form of pattern shown in the entire series and may be concentric or in part linear. This is shown in plates XII to XVIII and XXXVIII. The concentric extension at least would seem to constitute a sort of reverse principle to that illustrated by the changes in form resulting from my experimental conditions, such as high temperature. In dealing with definite directions of response which may be termed orthogenetic if desired, one must recognize progressive modification on the basis of a mechanism which may move in any one of two or three or more directions under the stress of external stimuli. Some evidence for a progressive series of modifications in the same direction running through a series of species in the tiger beetles is afforded by the experimental results. In general the pattern of *C. hirticollis* is more angular and as a whole conforms to the original ground plan better than that of *C. tranquebarica*. The modification of the patterns (middle band) of *C. hirticollis* is in a direction toward that of *C. tranquebarica*, but is not carried so far as are the modified patterns of *C. tranquebarica*. *C. limbalis* is usually, in the less modified forms of middle band, about as far from the original angular type as are the more modified forms of *C. tranquebarica*. Stimulation of the mechanism of the middle band in *limbalis* at this stage usually throws the band still further toward that of *splendida* or typical *purpurea* (Fig. 537, Pl. XXVIII). Since the middle bands of the three species differ normally only in the extent to which such oblique shifting occurs, and each differs from the original plan to a greater degree than the other, the peculiar character of the direction taken must result from a similarity of mechanism in the different species concerned. Abundant evidence for stages in such shifting as fixed hereditary

characters is found in many patterns illustrated in the plates, particularly plate XXXVIII. The series of three species thus show the same tendency, with respect to the middle band. This must be due to the existence of the same mechanism for heredity and response. The next step to important discovery probably lies in the direction of further analysis of the mechanism by experimental means, which may include surgical and mechanical experiments on the developing wing covers, and analysis by such methods are commonly used by the breeder.

#### BEARING OF THE PATTERN MECHANISM ON THE BIOGENETIC LAW

The data accumulated in connection with this study shows certain principles concerned with the application of the biogenetic law. First the general plan of the pattern seems to be common to all insects. The ancestry of the insect group is too obscure to justify the assumption that any original ancestor possessed a wing with nineteen spots such as are shown in the elytron of *Cicindela*, or that such an ancestor possessed longitudinal stripes or cross bands. The evidence seems to indicate that the tiger beetle group shows a type of pattern mechanism described at length in the preceding pages; that this pattern mechanism is plastic at least in the more generalized species; that from this plastic mechanism certain definite lines of modification have been somewhat fixed and limited. So long as the ontogenetic features are concerned with the general mechanism one is not justified in calling the appearance of certain spots recapitulations. They may fully as well be areas which are less favorably nourished or which are made up of cells with lower rates of metabolism (see p. 31). Either of these physiological conditions may be due to mechanical necessities in development in all insects primitive and specialized, and if so, why call them recapitulations?

Such evidences of recapitulation as do occur are found in the recurrence of markings in development which represent those occurring in related species or varieties. Thus, as I have noted, a curved middle band occurs in the ontogeny of some specimens of *C. lecontei* and duplicates a late stage in the loss of this marking as shown in figure 115, plate IX. Here a curved and degenerate form of this marking occurs temporarily during ontogeny and may perhaps be regarded as recapitulation. The application of the biogenetic law must generally be followed with great caution in dealing with insect patterns and no doubt with many other phenomena.

## SUMMARY OF CONCLUSIONS

## PATTERNS

1. The color patterns of the tiger beetles are related to elytral structures but not casually; longitudinal stripes in which pigment usually occurs lie in the area of the chief tracheal trunks; there are seven cross bands in which pigment does not develop, the second and third and fifth and sixth of these are often joined to make one of each pair.

2. Pigment usually occurs about the bases of hairs which usually lie in the lines of the tracheae.

3. In ontogeny the elytra show a spotted condition corresponding to the system of cross bands and longitudinal stripes. The longitudinal stripes are usually more pronounced.

4. The characteristic markings of the group are composed of spots or elements joined in the longitudinal light stripe areas and areas of cross bands with the loss of various spots or elements which occur in ontogeny; joinings are sometimes oblique and when so markings are sometimes parallel with curved end of the elytron.

5. Certain particular types of markings made up of a few elements joined in a particular way characterize the majority of species of the group.

6. These markings as derived from the cross and longitudinal bands are angular; reduction of angles, straightening and turning into oblique positions parallel with the end of the elytron characterize modifications of markings. The response to stimuli (high temperature) is in the same direction.

7. Response to other stimuli appears to be in the direction of concentric extension of the markings.

8. The color patterns and structure to which they are related constitute a mechanism, the directions of movement of which are limited, i.e., easier in some directions than others; the color pattern plans break when the related structures do; hereditary changes and fluctuations due to stimulation during ontogeny are in the same direction; laws governing the mechanism are the same throughout.

9. These laws when applied to hereditary changes are apparently what is sometimes termed *orthogenesis*.

10. It is not correct to assume that all manifestations of the wing mechanism which appear during ontogeny follow the biogenetic law.

## COLOR

1. The brilliant colors of the group are due to thin surface films of material having properties of metals.

2. Changes in color during ontogeny are from green and blue toward red or brown, except in *C. lepida* in which it is from yellow (gold) to green; purples appear to stand apart from greenish blues and do not change during ontogeny or if so only slightly.

3. During ontogeny some species pass through stages corresponding to geographic races, but the biogenetic law is of doubtful application, though green stages in ontogeny possess the same amount of pigment as green races and the reds and brown which come later are associated with more pigment but not causally.

## GEOGRAPHY

1. The center of distribution of the group is about the Indian Ocean.

2. Geographic races and geographic distribution is not correlated with any observed climatic or meteorological conditions unless it be rainfall and in this case the correlation is not complete. This lack of correlation is believed to be due to a lack of records of soil conditions.

3. Experimental modifications nearly duplicate certain geographic races of the species concerned; these races occur in localities where conditions are probably similar to the experimental condition.

4. In the species studied in detail the more brilliant colors are in warm arid localities, reduced marking in warm localities, and extended marking in cooler localities.

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## EXPLANATION OF PLATES

Because of the diversity of material studied, the plates of this monograph have been made in different ways and for details and exceptions to the general statements below it will be necessary to see the text. Plates I to IV show camera drawings made chiefly by mounting dry elytra in hot balsam containing little or none of the usual solvents. Plate V is a diagram. Plates VIII to XI were made from specimens killed in the best of fixing fluids and mounted according to approved methods. They represent different individuals chosen at different stages, but have been checked with individual histories. Plates VI, VII, and XII to XXVIII, in so far as they are concerned with elytra, are made up of free-hand drawings of elytra as seen from directly above the center of the curved side, i. e. to the left and above the specimen. The specimens represented are from various sources. All are drawn the same size though the specimens vary greatly. The drawings in plates XII to XVIII are about twice the natural size of an average species. The distribution data shown were supplied from various collections and printed lists. The colored plates which show color ontogeny were made chiefly from the same living individual.



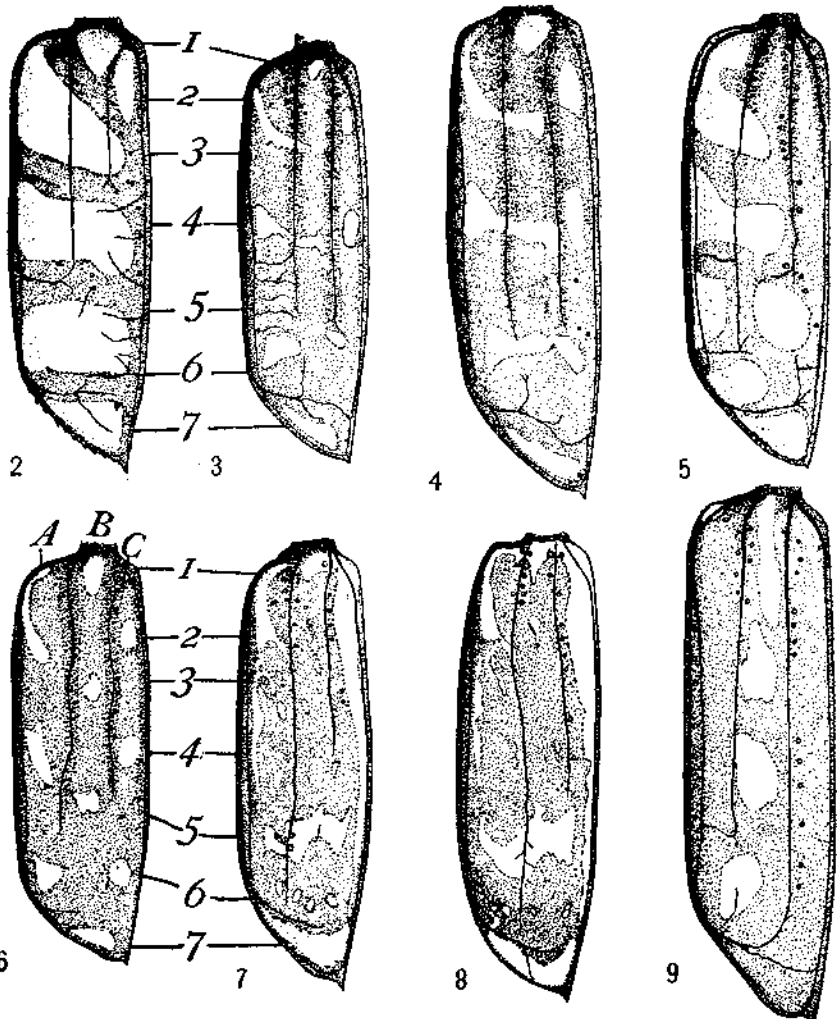
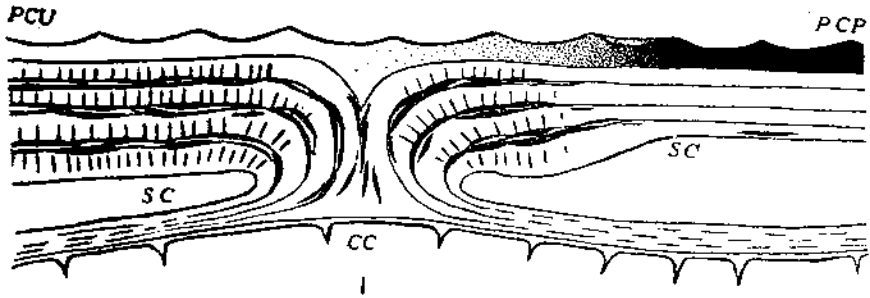
## PLATE I

## EXPLANATION OF PLATE

FIGURE 1. Cross section of the adult elytron of *C. lepida*, showing the relation of lack of pigment to interlamellar spaces. The portion at the right is through a pigmented area and that at the left through an unpigmented area. *PCU*, primary cuticula, unpigmented; *PCP*, primary cuticula, pigmented; *SC*, secondary cuticula. The portion under the unpigmented areas is divided into layers separated by air-filled spaces above which small canals project into the layer above; under the pigmented part the cuticula is in clear layers with no spaces between. The air spaces in the cuticula under the unpigmented portion are probably the cause of the appearance resembling white pigment in the unpigmented areas.

Figures 2-9. Showing the relation of the markings and tracheae in *Cicindela*. The tracheae present are from left to right costa (*Co*) (see Fig. 21), the subcosta (*S*), the radius (*R*), the media (*M*), and the cubitus (*Cu*). The anal cannot ordinarily be demonstrated in dried elytra. The drawings were made with a camera lucida. The figures indicate a number of unpigmented areas which are in the form of cross bands which may be broken by the pigment lying in the lines of the tracheae; the letters *A*, *B*, and *C* indicate the unpigmented stripes to fall between the tracheae.

Fig. 2. *C. regalis* Dej. (Africa); 3, *interrupta* Fabr. (Africa); 4, *interrupta* Fabr. (Africa); 5, *dougalensis* Klg. (N. Africa); 6, *vigintiguttata* Herbst. (India); 7, *compressicornis* Boh. (Africa); 8, *compressicornis* Boh. (Africa); 9, *discrepans* Walk. (Ceylon).

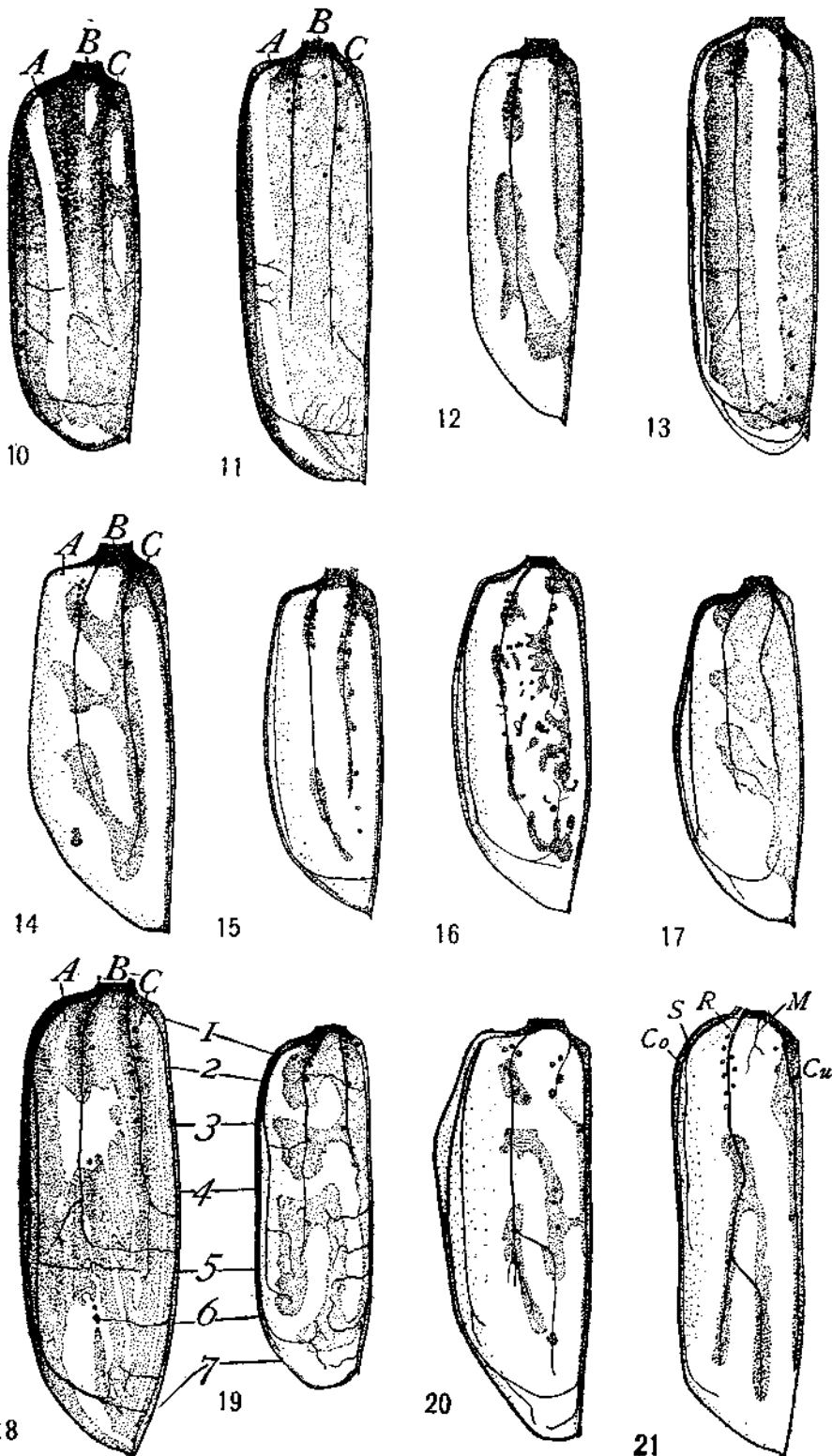


## PLATE II

FIGURES 10-21. Showing the close correlation between the distribution of tracheae and dark pigment in the more specialized patterns of *Cicindela*. Figures 10 to 22 show close conformation of color patterns and tracheae.

## EXPLANATION OF PLATE

Fig. 10. *C. striolata* Illig. (India); 11, *cincta* Oliv. (Africa); 12, *anchoralis* Chr. (S. China); 13, *quadri-lineata* Fabr. (India); 14, *capensis* Linn.—the costa and subcosta were probably present but could not be demonstrated; 15, *capensis* Linn. sub. sp. *chrysographa* Dej. (S. Africa); 16, *nivea* Kirb. aber *conspersa* Dej., showing reduction of the media (S. America); 17, *pamphila* Lec. (S. U. S.); 18, *lugubris* Dej. (Africa); 19, *gabbi* G. Horn (S. W. U. S.); 20, *dorsalis* Say (Coast of U. S. A.); 21, *tenuipes* Dej. (India), *Co*, costa, *S*, subcosta, *R*, radius, *M*, media, *Cu*, cubitus.



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COLORS OF TIGER BEETLES

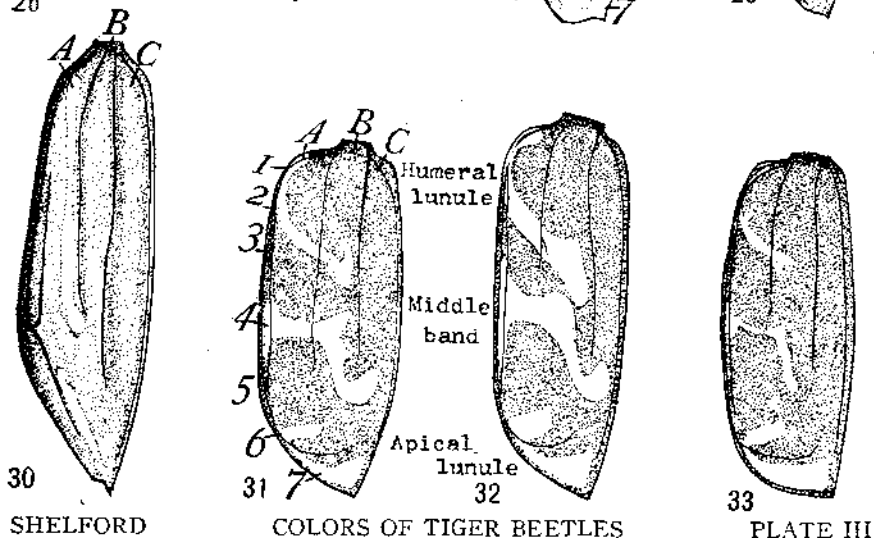
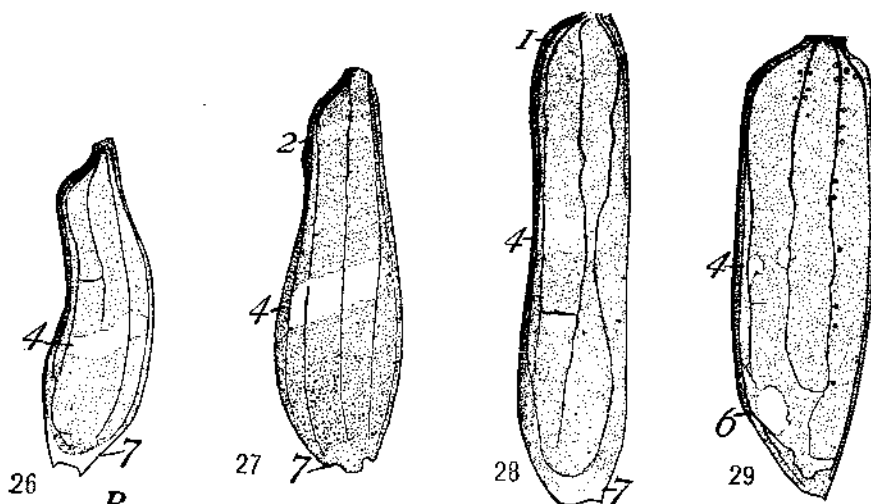
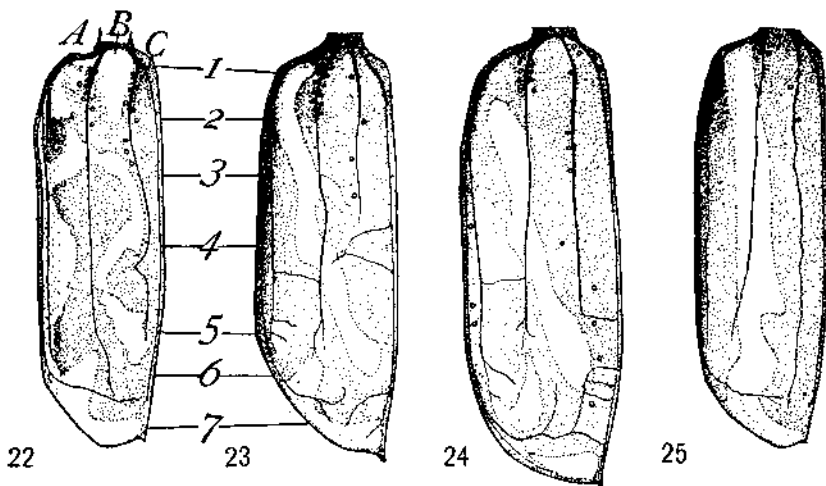
PLATE II

## PLATE III

FIGURES 22-33. Showing the transverse, longitudinal, and oblique bands in Ctenostomidae Collyridae; Cicindelidae (Dromicini and Odontochilini) and variations in the markings of *C. tranquebarica*, a species with typical patterns and variations.

## EXPLANATION OF PLATE

Fig. 22. *C. longipes* Fabr. (Malay Arch.); 23, *imperfecta* Lec. (S. W. U. S.); 24, *luteolineata* Chvr. (Mexico); 25, *lemniscata* Lec. (S. W. U. S.); 26, *Ctenostoma obliquatum* Chd. (South America), showing the central transverse band and distal spot; 27, *Ctenostoma unifasciatum* Dej. (S. America); 28, *Collyris celebensis* Chd. (Malay Arch.), showing three lighter cross bands; 29, *Heptodonta analis* Fabr. (India), showing spots representing two cross bands; 30, *Dromica coarctata* Dej. (S. Africa), showing longitudinal stripes and heavier pigment in the lines of the tracheae; 31-33, showing patterns of *C. tranquebarica* Herbst (N. A.), typical pattern (31) and extended pattern with extensions between the tracheae (32), and a reduced pattern (33) with the middle marking broken in the line of the trachea.



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COLORS OF TIGER BEETLES

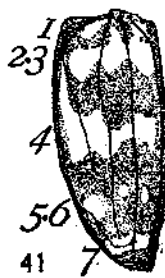
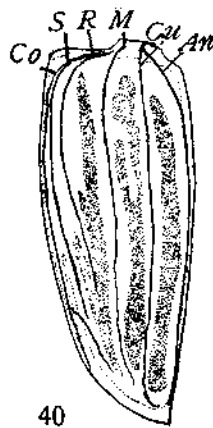
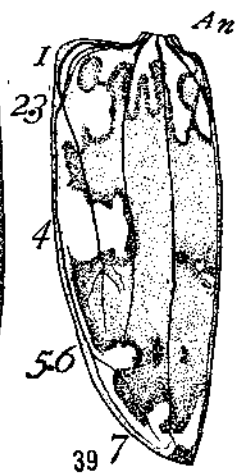
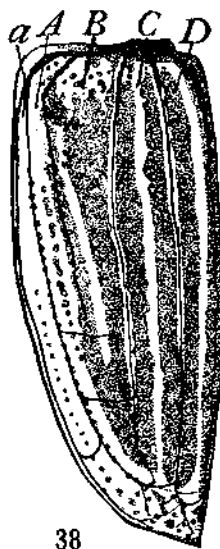
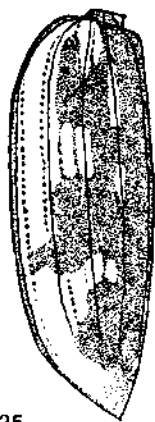
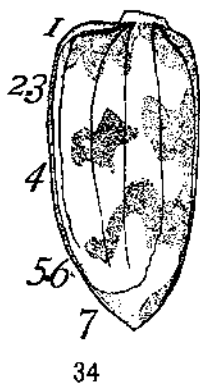
PLATE III

## PLATE IV

FIGURES 34-38. Showing the relation of the tracheae to pigmentation of the elytra in Carabidae and Dytiscidae.

## EXPLANATION OF PLATE

Fig. 34. *Omophron* sp. (N. A.), showing suggestions of transverse bands numbered to correspond with figures 66 and 67 and a tendency for white markings between the bands to lie between the tracheae; 35, *Bembidium versicolor* Lec. (Illinois), showing the unpigmented areas in the lines with the tracheae; 36, unknown carabid (Amazon), showing the pigmented areas in the lines of the tracheae; 37, *Nebia complanata* Linn. (Europe), showing a tendency to lines over the tracheae and between them; 38, *Hydacticus stagnalis* Fabr. (Illinois), showing double lines; 39, *Laccophilus maculosus* Say, showing the transverse bands and suggestion of double unpigmented lines with the tracheae in the pigmented areas (see Fig. 18); 40, *Agabus taeniolatus* Harr. (Illinois), showing trachea in the unpigmented areas with a suggestion of double lines; 41, *Hydroporus undulatus* Say (Illinois), showing the cross bands—a suggestion of all those commonly present in *Cicindela*.



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COLORS OF TIGER BEETLES

PLATE IV



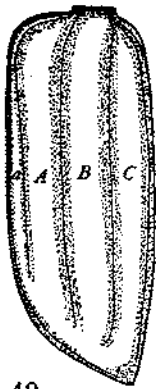
## PLATE V

FIGURES 42-49. Showing an analysis of the color patterns of *Cicindela*.

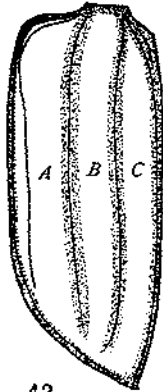
## EXPLANATION OF PLATE

Fig. 42. Showing the full number of longitudinal stripes represented in the group—compare with figures 169, 169a, and 169b (*tetragramma* Boisd.); 43, showing the three longitudinal stripes nearly always represented—compare with 52 (*C. tetragramma*, variation) and 54, *desgodinsi* Fair (Tibet); 44, showing the splitting of the stripes as suggested in 53, *lugubris* Dej. (Africa); 45, showing the full number of cross bands numbered 1 to 7; 46, showing the commonest cross bands illustrated in 58 (*regalis* Dej. Africa); 47, showing a second common type illustrated by 75, in which none of them reach clear across; 48, showing all the possible spots that can occur from a combination of the longitudinal stripes and cross band shown in figures 42 to 47; 49, showing the spots which are most commonly present or joined to form characteristic patterns in the group.

*A* and *a* are usually fused on account of the crowding together of the tracheae. The cross bands are never all represented entirely across the elytron, but by dots as in 62, *C. vigintiguttata* Herbst (India). The fusion of *A*<sub>1</sub>, *A*<sub>2</sub> and *B*<sub>3</sub> gives the characteristic humeral lunule of students of the group, the hook frequently present is made by joining it with *B*<sub>2</sub>. The fusion of *C*<sub>1</sub> and *C*<sub>2</sub> and of *C*<sub>3</sub> and *C*<sub>4</sub> gives the characteristic markings shown in the line *C*. of many old world species. The union of *A*<sub>4</sub>, *B*<sub>4</sub> and *B*<sub>5</sub> gives the characteristic middle band of the group. *A*<sub>3</sub> is of rare occurrence (see Fig. 198). *A*<sub>5</sub> is commonly present as a spot, also *A*<sub>6</sub>, *B*<sub>6</sub> and *C*<sub>6</sub> are less common in occurrence (see Figs. 6 and 7, Pl. I).



42



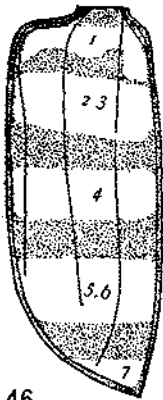
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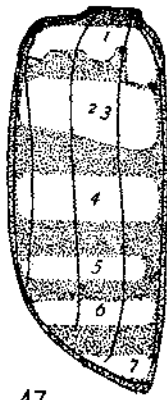


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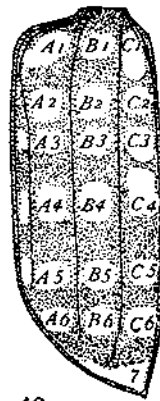
46

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47

COLORS OF TIGER BEETLES



48

Humeral lunule

Middle band

Apical lunule



49

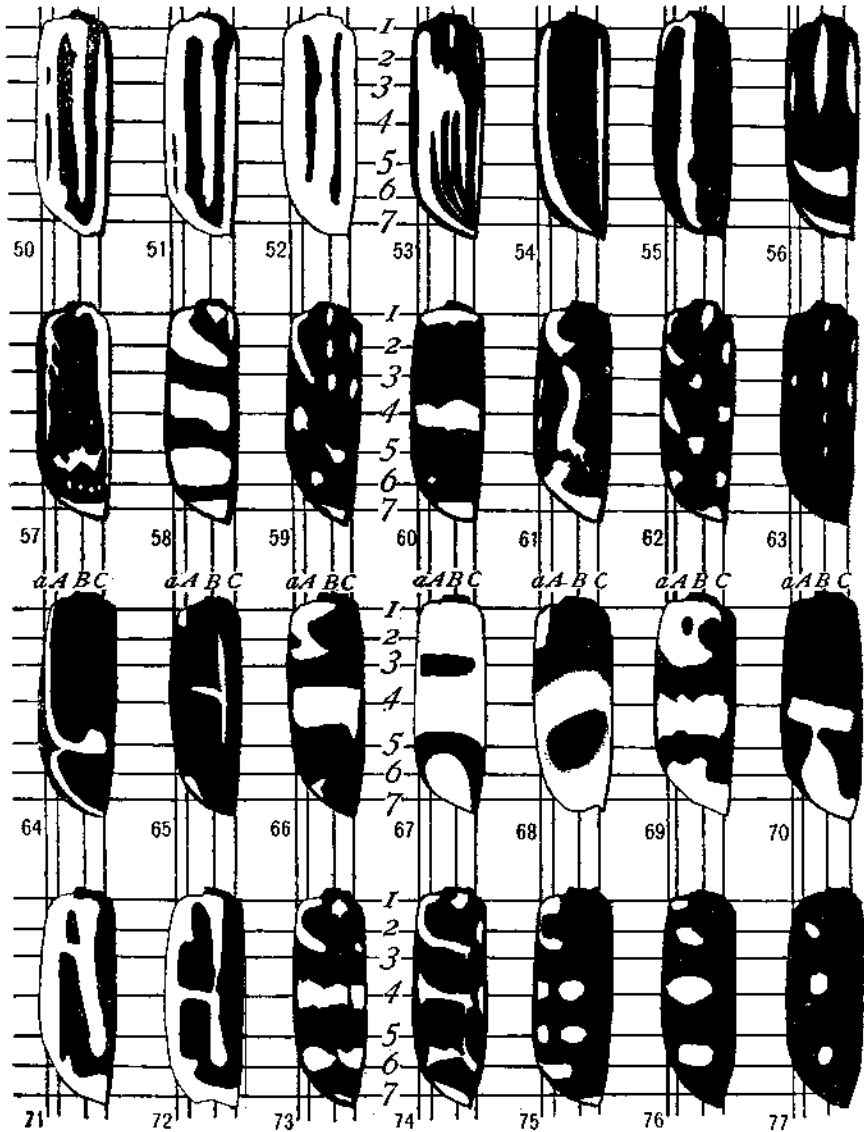
PLATE V

## PLATE VI

FIGURES 50-77. Showing selected Cicindelid patterns with lines to show the correspondence of all the chief types of pattern to the plan shown in Plate V.

## EXPLANATION OF PLATE

Figs. 50, 51, 52, *C. tetragramma* Boisd. (Australia); 53, *lugubrus* Dej. (Africa); 54, *desgodinsi* Fair (Tibet); 55, *interruptofasciata* Schm. (Siam); 56, *muata* sub. sp. *laticornis* Horn (Africa); 57, *compressicornis* Boh (Africa); 58, *regalis* Dej. (Africa); 59, *atkinsoni* Gestro (Australia); 60, *regina* Kolbe (Africa); 61, *melaleuca* Dej. (S. A.); 62, *vigintiguttata* Herbst (India); 63, *notata* Boh (Africa); 64, *gerstaeckeri* Horn (Africa); 65, *Euryoda adonis* subsp. *rufosquata* Bell (Madagascar), Boh; 66, *siamensis*, (Siam); 67, *Odontochila singularis* Flt. (S. A.); 68, *Peridexia hilaris*, Fairm. (Madagascar); 69, *flavosignata*, Cast. (Africa); 70, *crepigny*; Bates (Borneo); 71, *anchoralis* Schm. (China); 72, *copulata* Schm. (India); 73, *interrupta* subsp. *gabonica* Bat. (Africa); 75, *aphrodisia* Baudi (Cypris); 76, *aurulenta* Fabr. (India); 77, *6 punctata*, Fabr. (India).



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COLORS OF TIGER BEETLES

PLATE VI

## PLATE VII

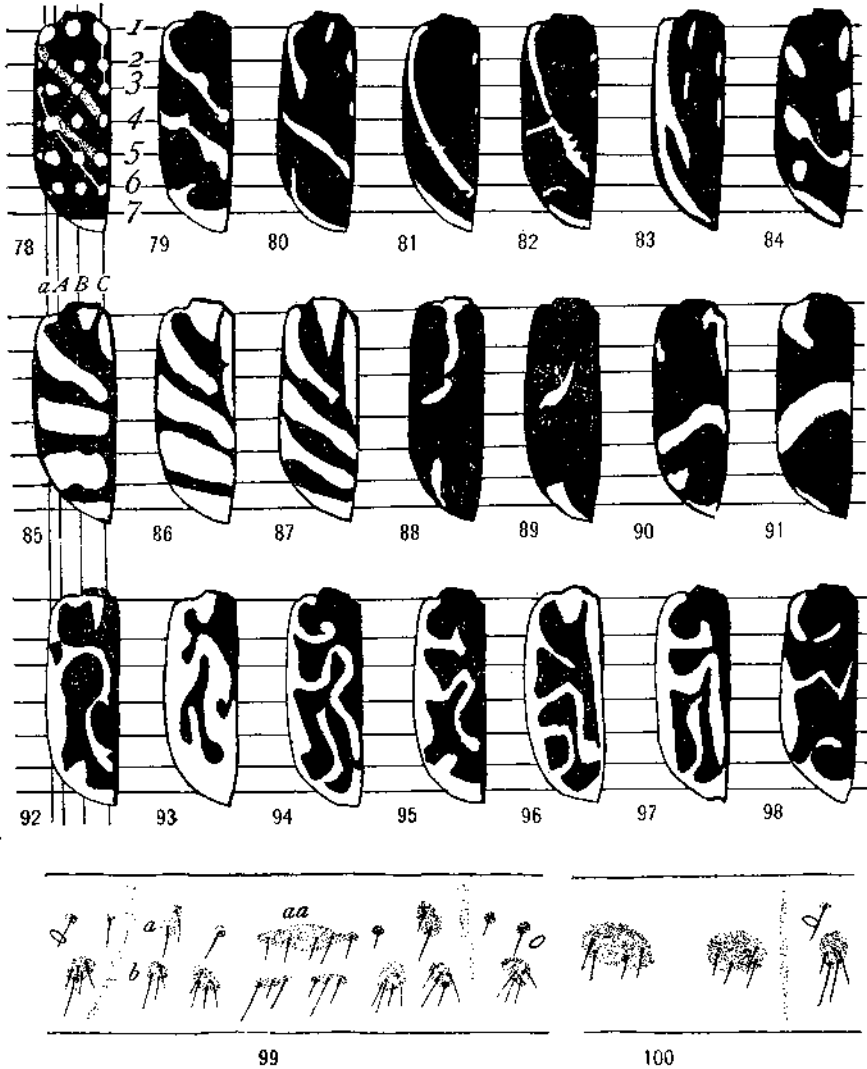
FIGURES 78-98. Showing some of the chief lines of union of markings not indicated on the preceding chart.

## EXPLANATION OF PLATE

Fig. 78, showing the spots which enter into the patterns with some of the characteristic unions indicated—the stippled areas refer to figures 79 and 80; the narrow white lines to 81, 82, and 83; the dotted lines to 88 and 89, and 90 and 91; 79, *apiata claussemi* Putz (S. A.); 80, *striolata* subsp. *tresignata* Chd. (India); 81, *fatidica* Guer (Africa); 82, (*Prodoles*) *minula* Per. (Africa); 83, *viridis* Raffr. (Africa); 84, *peletieri* (N. Africa).

Figs. 85-87. Showing the oblique shifting of the cross markings; 85, *regalis* Dej. (Africa); 86, *andriana* All (Africa); 87, *makeva* Kunck (Africa); 88, *ceylonensis* Horn (India); 89, *oscar* Horn (Africa); 90, *kolbei* Horn (Africa); 91, *princeps ducalis* Horn (India); 92, *longipes* Fabr. (Malay Arch.); 93, *albicans* Chd. (Australia); 94, *nitida* Wdm. (India); 95, *tresignata* Dej. (Europe); 96, *nitidula* Dej. (Africa); 97, *gabbi* S. Horn (S. W. U. S. A.); 98, *leuconoe*, Bates (Mexico).

Figures 99-100. Showing the color areas of the larvae for comparison with figures 101 to 105. Ventral side of the abdominal segment of a larva of *C. tranquebarica*. The areas are lettered as in figure 101; 100, showing the color centers of the dorsal side of a larva. Compare with figure 101. The area with the spiracles is the pleuron.



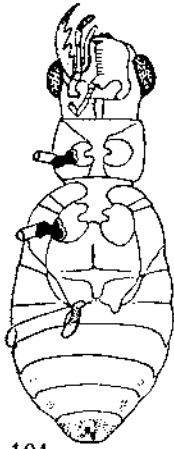
## PLATE VIII

FIGURES 101-110. Showing the development of pigment in the legs and body of *C. tranquebarica*, Herbst.

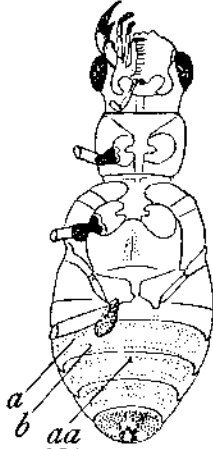
## EXPLANATION OF PLATE

Figures 101-110. Showing the pigment beginning at the posterior end of the body and moving forward except the trochanters which are pigmented at emergence; 101, 3 to 6 hours after emergence; 102, 8 to 12 hours; 103, 12 to 15 hours; 104, 24 to 36 hours. *A*, anterior band of pigment on the segment; *f*, the posterior band of the segment; *aa*, the large central anterior area—compare with figure 105.

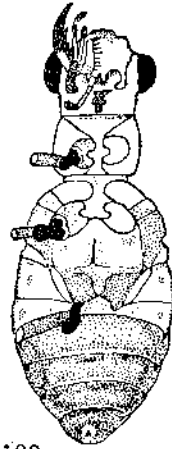
Figs. 105-108, showing the development of pigment in the dorsal side of the abdomen; 105, at emergence, showing the large dorsal spots beginning of the posterior segments; 105*a*, after 3 to 6 hours, showing the fusion of the spots toward the center; 106, 8 to 10 hours after emergence, showing the nearly complete abdominal pigment, the beginning of the pigmentation of the thorax, and the lines on the head; 107, showing the increase in the head and thoracic regions at 12 to 15 hours after emergence; 108, showing the dorsal side of the head and thorax after 24 to 36 hours; 109 *a* to *d*, the antenna; 3 hours after emergence; *b*, 6 hours after emergence; *c* at 8 to 10 hours after emergence; *d*, 11 to 15 hours after emergence; *e*, 24 hours after emergence; 110, *a*, showing the hind leg three days after emergence; *b*, at emergence; *c*, after 6 to 8 hours; *d*, 12 hours after emergence.



101



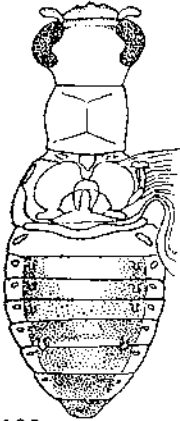
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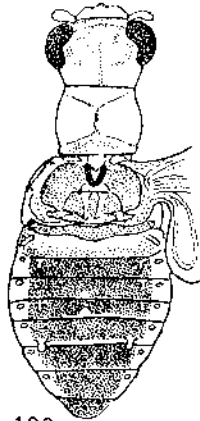
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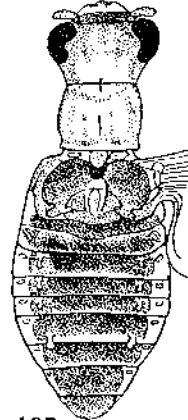
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105 a



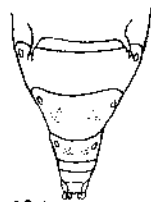
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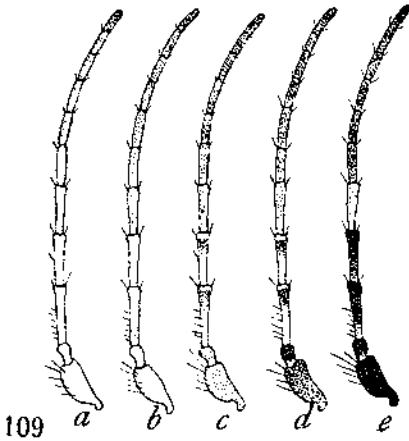
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105



109



110



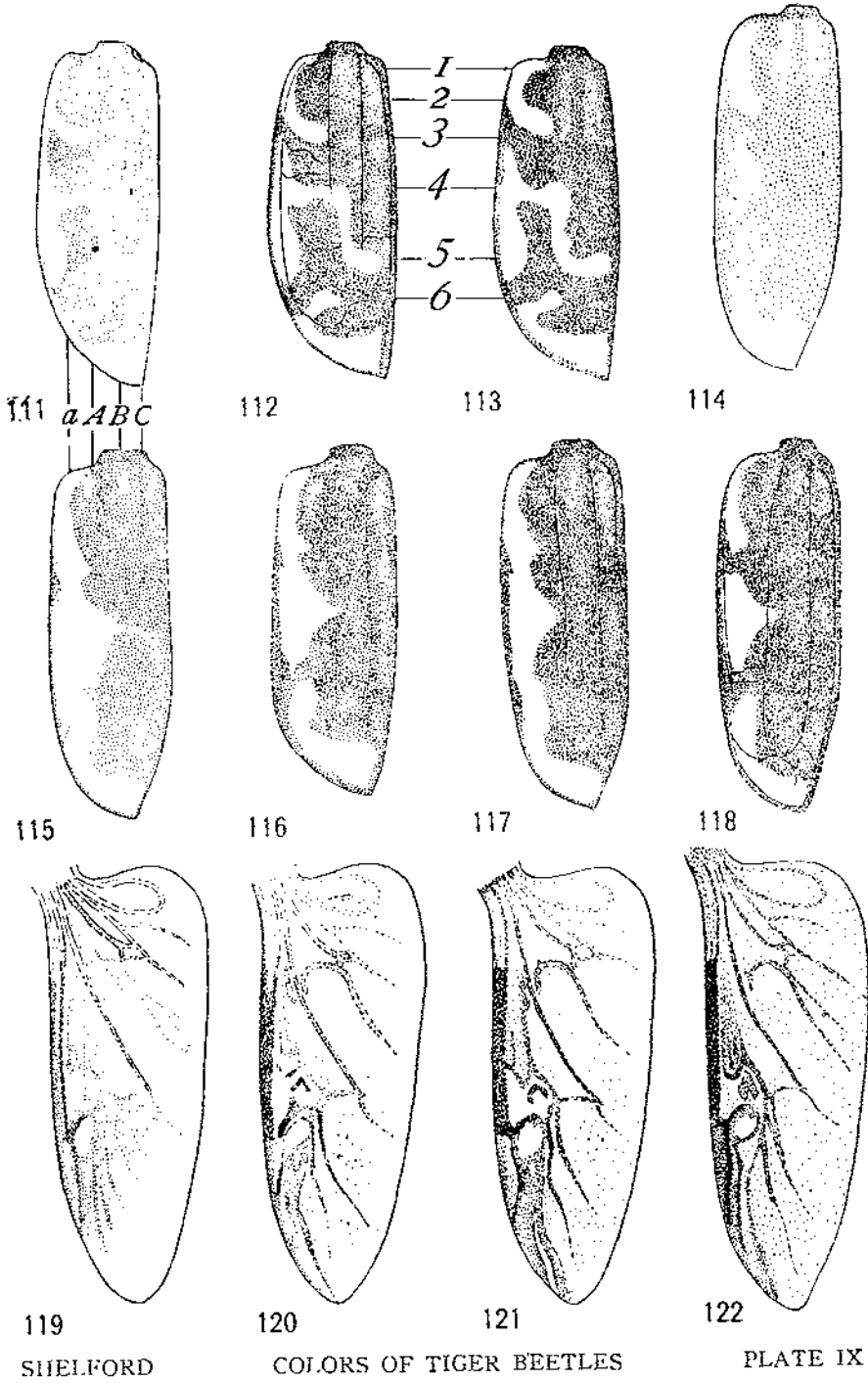


## PLATE IX

FIGURES 111-122. Showing stages in the development of pigment in the clytron of *C. repanda* Dej. and *C. scutellaris* aber *lecontei* Hald.

## EXPLANATION OF PLATE

Fig. 111, 4 to 5 hours after emergence, showing the longitudinal lighter areas corresponding to *A*, *B*, *C* of the preceding figures; 112, after 12 to 15 hours, showing the stripes *A*, *B*, *C* broken into cross bands, 3 and 4 being clearly indicated in the stripe *C*; 114-118, showing stages in the development of the clytral pigment in *C. scutellaris lecontei* Hald; 114, after 4 to 5 hours; 115, after 12 hours, showing particularly a well indicated cross band not appearing in the adult; 116, after 15 hours, showing well marked longitudinal bands broken in spots; 117, after 36 hours with similar marking indicated; 118, after 36 hours, similar to 117; 119, the hind wing at emergence; 120, after 12 hours; 121, after 36 hours; 122, adult.



## PLATE X

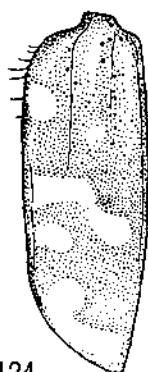
FIGURES 123-134. Showing stages in the development of the pigment of the elytra of *C. purpurea limbalis* Klg. (123-130), and in *C. tranquebarica* Herbst (131-134). The wing areas are indicated by letters and numbers as in the preceding figures.

## EXPLANATION OF PLATE

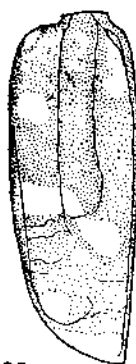
FIG. 123. Three hours after emergence, showing the lighter areas between the tracheae; 124, after 8 hours—suggestion of both longitudinal stripes transverse bands; 125, showing a similar condition after 10 hours; 126, similar conditions at the end of 12 to 15 hours; 127, a similar suggestion of markings at 30 hours; 128, well defined markings at 36 hours; 129, striking longitudinal stripes at 36 hours; 130, heavier pigmentation in the lines of the trachea in the adult; 131 to 134, showing a similar series for the development of pigment in *C. tranquebarica* Herbst; 131, 6 to 8 hours after emergence; 132, 10 hours after emergence; 133, 12 hours after emergence; 134, 24 to 36 hours after emergence.



123



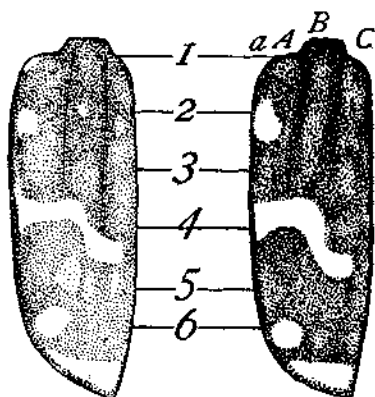
124



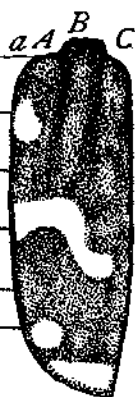
125



126



127



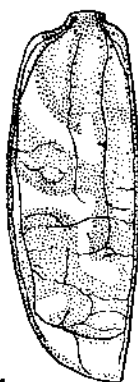
128



129

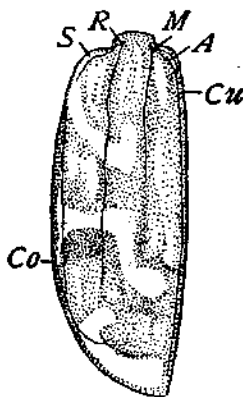


130



131

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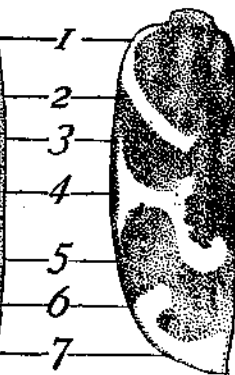


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COLORS OF TIGER BEETLES



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PLATE X

## PLATE XI

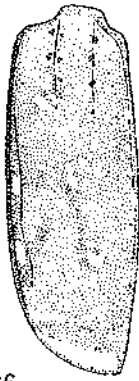
FIGURES 135-146. Showing the ontogeny of pigmentation in *C. punctulata* Oliv., *C. sexguttata* Fabr., *Tetracha carolina* Linn., *C. hirticollis* Say, and *C. 12 guttata* Dej.

## EXPLANATION OF PLATE

Fig. 135, *C. punctulata* Oliv. at the end of 6 hours after emergence; 136, after 12 to 13 hours; 137, after 36 hours; 138, *sexguttata* Fabr. after 24 hours; 139, *Tetracha carolina* Linn. at the end of 9 hours after emergence; 140, the adult elytron; 141-145, showing stages in the development of pigment in *hirticollis* Say; 141, 4 hours after emergence; 142, after 6 to 10 hours; 144, after 12 hours; 145, after 16 to 24 hours; 146, *12 guttata*, after 12 to 18 hours.



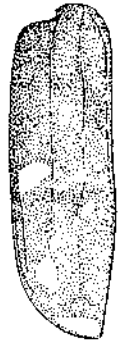
135



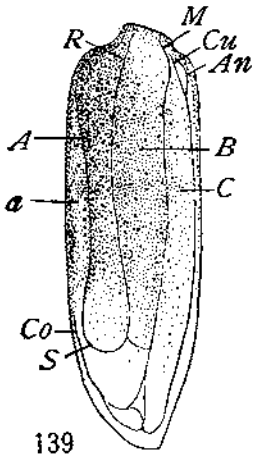
136



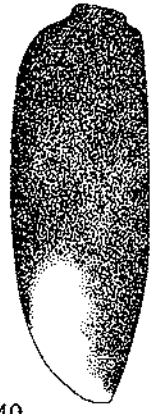
137



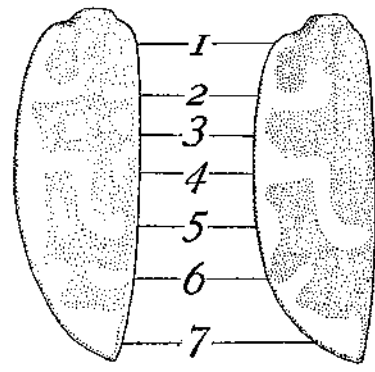
138



139



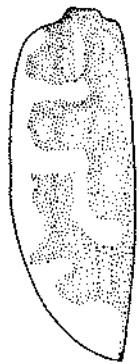
140



141

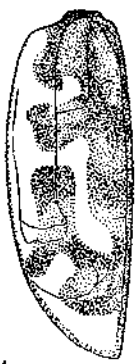


142



143

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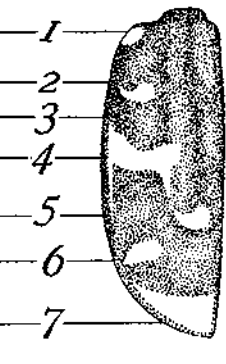


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PLATE XI

## PLATE XII

FIGURES 147-187. Showing patterns made up of longitudinal and transverse bands variously broken and contrived. Follow the arrows in tracing out the different directions of modification. For meaning of letters see page 9.

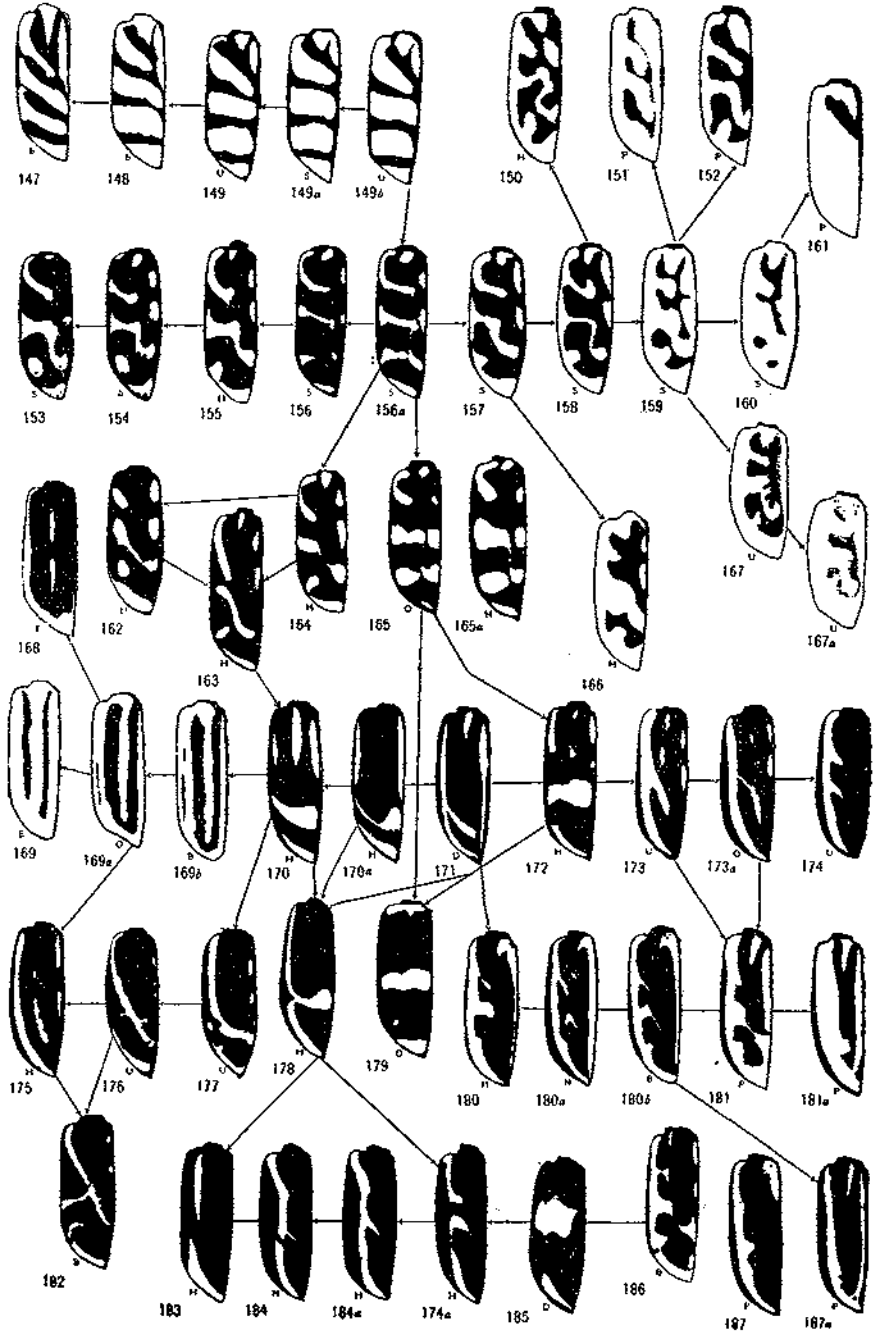
## EXPLANATION OF PLATE

Figs. 147-149*B*, showing the typical transverse wide transverse band type of pattern and modifications; 147, *maheva* Kunck. (Madagascar); 148, *andriana* All. (Madagascar); 149, *regalis* Dej. (Africa); 149 *a* and *b*, the same.

Figs. 150-167*a*, showing *interrupta gabonica* type of broken transverse bands and their modification. The patterns of *gabonica* 165 and 165*a* are made up of transverse bands and broken in the lines of the tracheae with various lines of longitudinal and transverse union.

Figs. 150-152, showing the unusual patterns belonging to this group; 150, *singularis* Chd. (N. E. Africa); 151, *kollari* Gistl. (S. Africa); 152, *malaris* Horn (S. A.); 153 and 154, *flexuosa* Fabr. (Europe); 155, *striatifrons* Chd. (India); 156-156*a*, *interrupta* Fabr. (Africa); 157, *monteiroi* Bat. (S. Africa); 158, *brevicollis* subsp. *clathrata* Dej. (Africa); 159-160, *candida* Dej. (Africa); 161, *blanchardi* Fairm. (S. Africa); 162, *pelletieri* Luc. (N. Africa); 163, *vittigera* Dej. (India); 164, *multiguttata* Dej. (India); 165, *interrupta* Fabr. subsp. *gabonica* (Africa); 165*a*, *interrupta* Fabr. subsp. *gabonica*; 166, *laetescripta* Mtsch. (E. Asia); 167, *lepida* Dej. (Illinois).

Figs. 168-169*a*, showing pattern with three longitudinal stripes; 168, *queenslandica* Sloane (Australia) (After W. Horn); 169*a*, *tetragramma* Boisd. (Australia); 170-170*a*, *muata* subsp. *laticornis* Horn (Africa); 171, *muata* Horn (Africa); 172, *juno* Horn (Africa); 173, 173*a*, *viridis* Raff (Africa); 174, *gigantea* Raffr. (Africa); 175, *prodotiformis* Horn (Africa); 176, *fatidica* Guer. (Africa); 177, *miseranda* Horn (Africa); 178, *gerstaeckeri* Horn (Africa); 179, *regina* Kolbe (Africa); 180-180*a*, *b*, *mechowi* Lued (Africa); 181-181*a*, *brazzai* Flt. (Africa); 182, *minula* Per. (Africa); 183, *quadristriata* Horn (Africa); 184-184*a*, *petiti* Guer. (Africa); 174*a*, *gigantea* Raffr. (Africa); 185, *junkeri* Kolbe (Africa); 186, *vittata* Fabr. (Africa); 187-187*a*, *congeensis* Flt. (Africa).



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PLATE XII

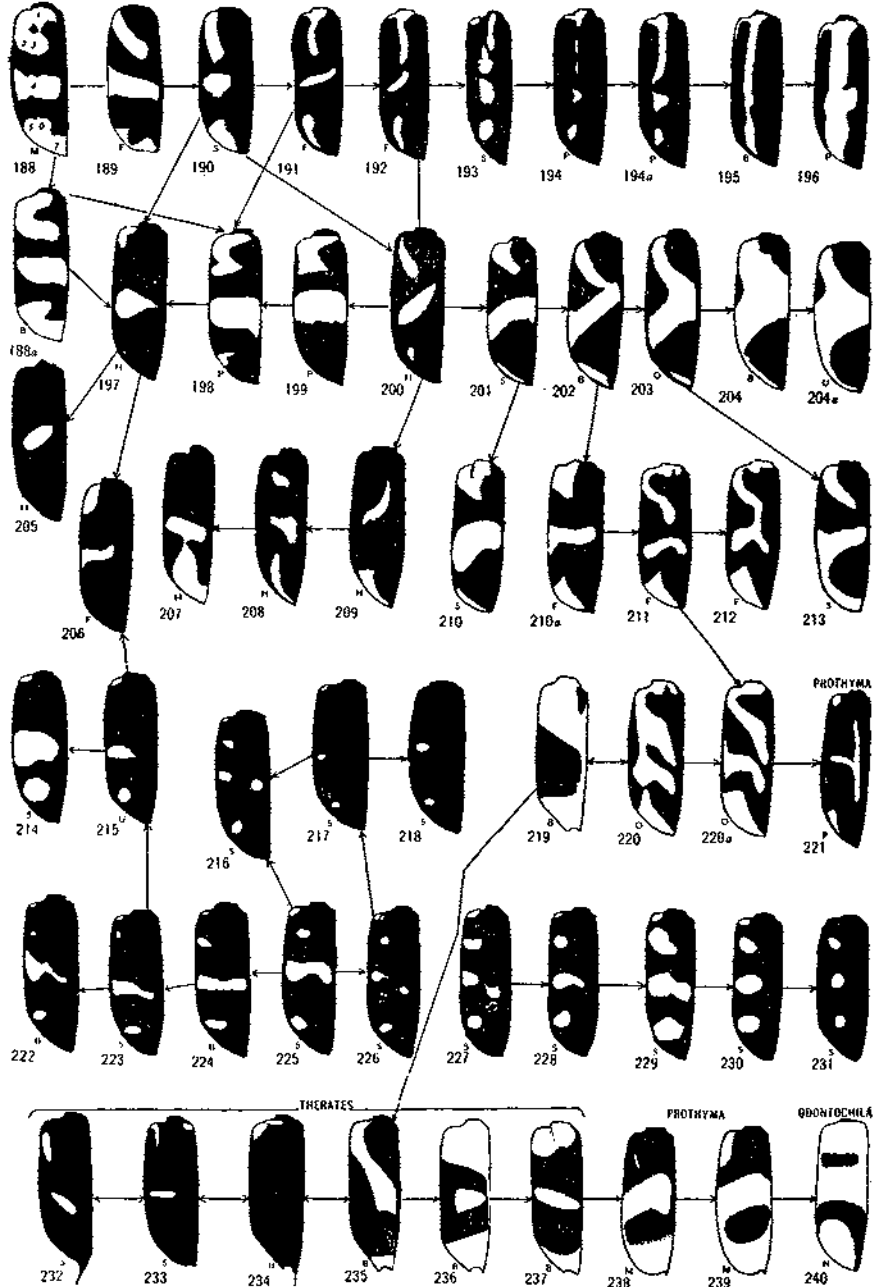


## PLATE XIII

FIGURES 188-240. Showing the domination of the central stripe (*B*), obliquity in the middle band reversed from the usual type. For meaning of letters see page 9. Follow the arrows in tracing out the different lines of modification. Figures 188 and 188a show the reduced transverse bands—compare with 149.

## EXPLANATION OF PLATE

Fig. 188 and 188a, *C. flavosignata* Cost. (Africa); 184, *dives* Gory, after Gory (India); 190, *aurovittata* Brll. (India); 191, *ceylonensis diversa* Horn, after Horn (India); 192, *ceylonensis* Horn, after Horn (India); 193, *discrepans* Wak (India); 194 and 194a, *harmandi* Flt. (India); 195, 196, *interruptofasciata* Schm. (India); 197, *assamensis* Parry (India); 198-199, *siamensis* Flt. (India); 200, *andrewesi mauritti* Horn (India); 201, *princeps ducalis* Horn (India); 202, *aurofasciata* Dej. (India); 203, *aurofasciata* Dej. (India); 204-204a, *aurofasciata lepida* Gory (India); 206, *assamensis* ?; 207, *crepignyi* Bat. (Malay Islands); 208, *kachovskiyi* Horn (Africa); 209, *askari* Horn (Africa); 210-210a, *shivah* Parry (India); 211-212 (After Schaum), *calligramma* Schut. (India); 213, *aurofasciata* Dej. (India); 214, *haemorrhoidalis* Wdm. (India); 215, *burmeisteri* Fischer (Asia); 216, *stenodora* Schm. (Malay Arch.); 217, *minuta* Oliv. (India); 218, *craspedota* Schm. (Borneo); 219, *semperi* Horn (India); 220, *calligramma* Schm. (India); 221, *Prothyma adonis rufosignata* Brll. (Madagascar); 222, *chinensis japonica* Thnb. (Japan); 223, *chinensis* DeG. (China); 224, *duponti* Dej. (India); 225, *exima* Vand. (Malay Arch.); 226, *ferrici* Flt. (Japan); 227, *didyma* Dej. (Malay Arch.); 228, *aurulenta* Fabr. (India); 229, *notata* Wdm. (India); 230, *aurulenta* Fabr. (India); 231, *punctata* Fabr. (India); 232, *Therates whiteheadi* Bates (Malay Arch.); 233, *T. fruhstorferi* Horn (Tonkin); 234, *T. spinipennis* Latr. and Dej. (Malay Arch.); 235, *T. chaudi* Schm. (Malay Arch.); 236, *T. maindroni* Horn (Malacca); 237, *T. erinys* Bates (Malay Arch.); 238, *Peridoxia hilaris* Fair. (Madagascar); 239, *Peridoxia fulvipes* Dej. (Madagascar); 240, *Pometon singularis* Flt. (S. A.).

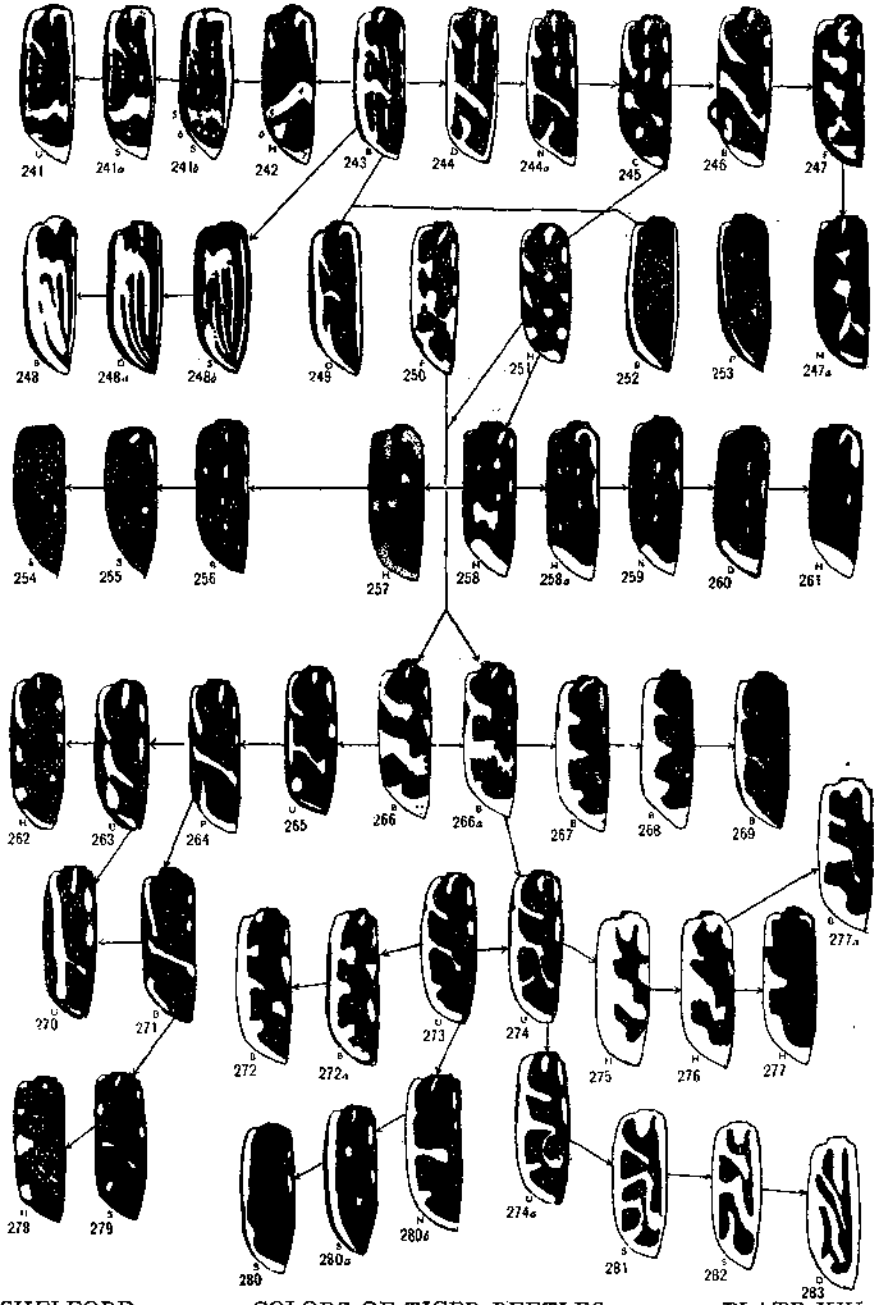


## PLATE XIV

FIGURES 241-283. Showing patterns made up of numerous spots and stripes. Figures 241 to 243 and 248, 248a, and 248b should be compared with plate IV, figure 38. In comparing the figures follow the arrows. For meaning of letters see page 9.

## EXPLANATION OF PLATE

Figs. 241-241a, b, *C. compressicornis*, Beh. (Africa); 242, *kolbei* Horn (Africa); 243, *deyrollei* Guer. (Africa); 244, *maino* Gestro (N. Guinea); 245, *atkinsoni* Gestro (India); 246, *feisthameli* Guer. (Africa); 247 (after Guerin)-247a, *nysa* Guer. (Liberia); 248, 248a, 248b, *lugubris* Dej. (Africa); 249, *deyrollei* Guer. (Africa); 250, *vittata* Fabr., after Guerin (Africa); 251, 20 *guttata* Herbst (India); 252, *desgodinsi* Fair. (Tibet); 253, *latreillei* Guer. (Kapaur)—the stippled spots are dark and represent areas in which spots usually occur; 254-255, *rasticana* Per. (S. Africa); 256, *notata* Boh. (S. Africa); 257, *latreillei* Guer. (Kapaur); 258-258a, b, *rasticana* Per. (S. Africa); 259, *rasticana* aber *egregia* Per. (S. Africa); 261, *bioncani* subsp. *liengmei* Per. (S. Africa); 262-263, *striolata* Ill. (Burmah); 264, *striolata* subsp. *trisinata* Chd. (Timor); 265, *neumanni* Kolbe (Africa); 266, *pubica* Boh. (Zulu); 266a, Boh. (Transvaal); 267-268, *escheri* Dej. (S. Africa); 269, *marginella* Dej. (Africa); 270, *striolata* Ill. (India); 271, do subsp. *trisinata* Chd. (Timor); 272, *luxeri* Dej. (Africa); 273, *heros* Fabr. (Malay Arch.); 274-274a, *heros* Fabr. (Malay Arch.); 275-277a, *monteiroi* Bat. (Africa); 278-279, *strachani* Hope (Africa); 280-280a, b, *equestris* Dej. (Madagascar); 281, *nitidula* Dej. (Africa); 282, *nilotica* Dej. (Africa); 283, *albina* Wdm. (India).



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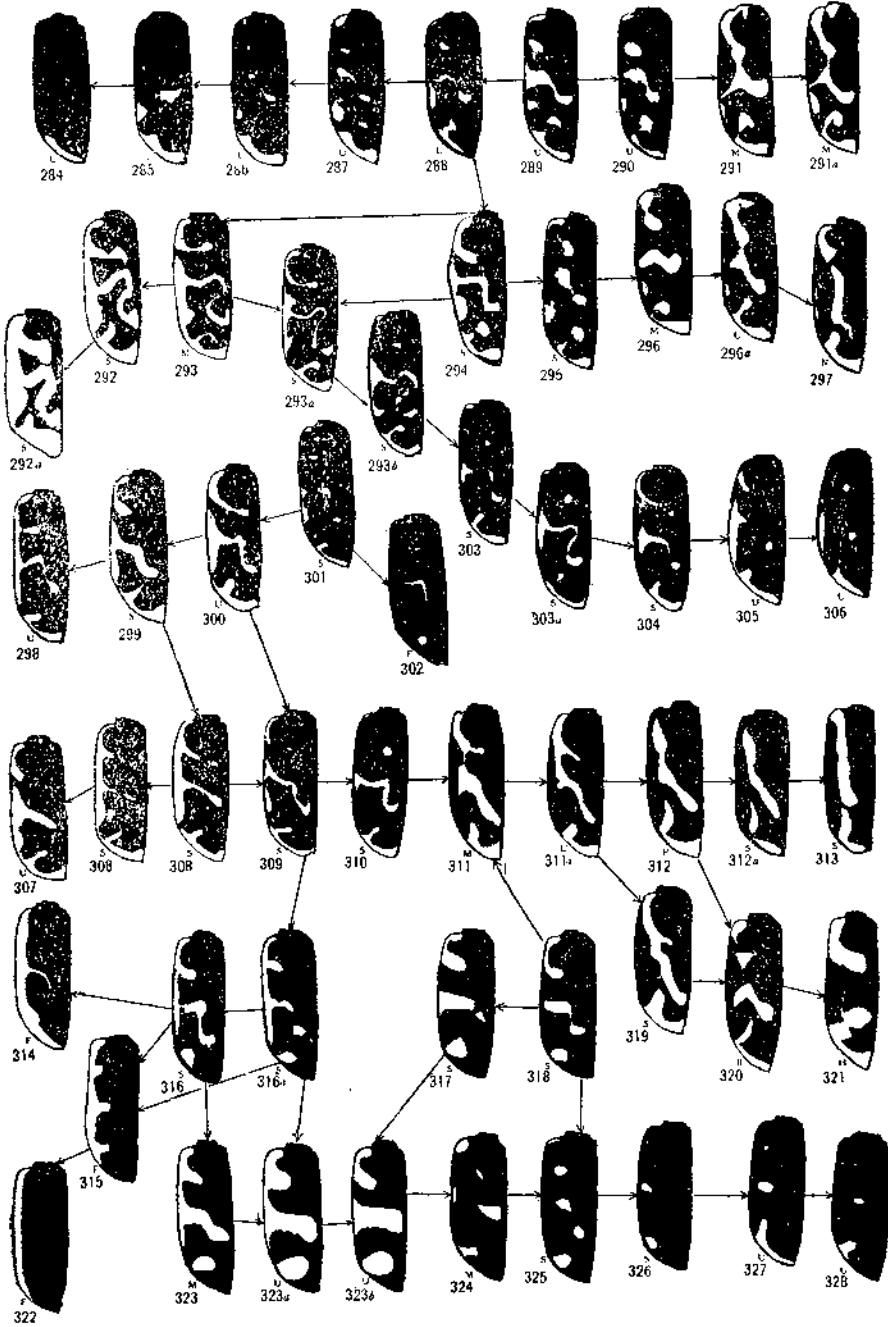
PLATE XIV

## PLATE XV

FIGURES 284-328. Showing the patterns of North American species belonging chiefly to the Mexican and *C. argentata* groups and having cross bands 5 and 6 both distinctly represented in the majority. For meaning of letters see page 9. Various combinations of spots which go to make up the oblique vitta of some of the species of the group are represented in figures 291, 296, 297, 311, 312, 313, 319, and 320; compare these with figures 23 and 24 and 78 to 82.

## EXPLANATION OF PLATE

Fig. 284, *C. polita* Lec. (Texas); 285, *abdominalis* Fabr. (Atlantic coast, U. S.); 286, *rufiventris* aber. *cumatilis* Lec. (Texas); 287, *rufiventris* Dej. (Eastern U. S.); 288, *16 punctata* Klg. (N. Mex.); 289, *carthagena* subsp. *hentsi* G. Horn (Mass.); 290, *16 punctata* Klg. (Mexico); 291-291a, *rufiventris* aber. *mellyi* Chd. (Mexico); 292, *trifasciata* Fabr. (S. A.); 293-293a, *b*, *trifasciata* subsp. *sigmoidea* Lec. (S. U. S.); 294, *carthagena* Dej. (Mexico); 295, *rufiventris* subsp. *16 punctata* Klg. (Mexico); 296, *rufiventris* aber. *mellyi* Chd. (Mexico); 297, *melaleuca* Dej. (S. A.); 298, *obsoleta* Say (S. W. U. S.); 299, *fera* Chv. (Mexico); 300, *pusilla* subsp. *cinctipennis* Lec. (S. W. U. S.); 301, *punctulata* Oliv. (U. S. and Mex.); 302, *argentata* subsp. *aureola* Klg. (S. A.); 303-303a, *argentata* Fabr. (Brazil); 304, *lunalonga* Schm. (California); 305, *celeripes* Lec. (Central U. S.); 306, *curvitans* Lec. (Miss. Valley); 307, *schaupii* G. Horn (Texas); 308-308a, *nephelota* Bat. (Mexico); 309-309a, *chlorostricta* subsp. *staudingeri* Horn (S. A.); 310, *argentata* subsp. *venustula* Gory (Mexico); 311-311a, *pusilla* subsp. *imperfecta* Lec. (Pacific States); 312, *luteolineata* Chvr. (Mexico); 313, *lemniscata* Lec. (Arizona); 314, *debilis* Bates, after Bates (Mexico); 315, *favengeri* Brill., after Andouin and Brullé (S. A.); 316, 316a, 317, *roseiventris* Chvr. (Mexico); 318, *flavopunctata* Chvr. (Mexico); 319, *pusilla* subsp. *imperfecta* Lec. (Pacific States); 320, *craveri* Thms. (Mexico); 321, *marquardtii* Horn—the only Cicindelid without a middle band (Sao Paulo); 322, *hoegi* Bat. after Bates (Mexico); 323-323a, *b*, *sommeri* Mann. (Mexico); 324, *anulipes* Horn (S. A.); 325, *flavopunctata* Chvr. (U. S. and Mexico); 326, *chrysilpe* Bates (Mexico); 328, *severa* Laf. (Gulf States and N. M.); 328, *striga* Lec. (Florida).



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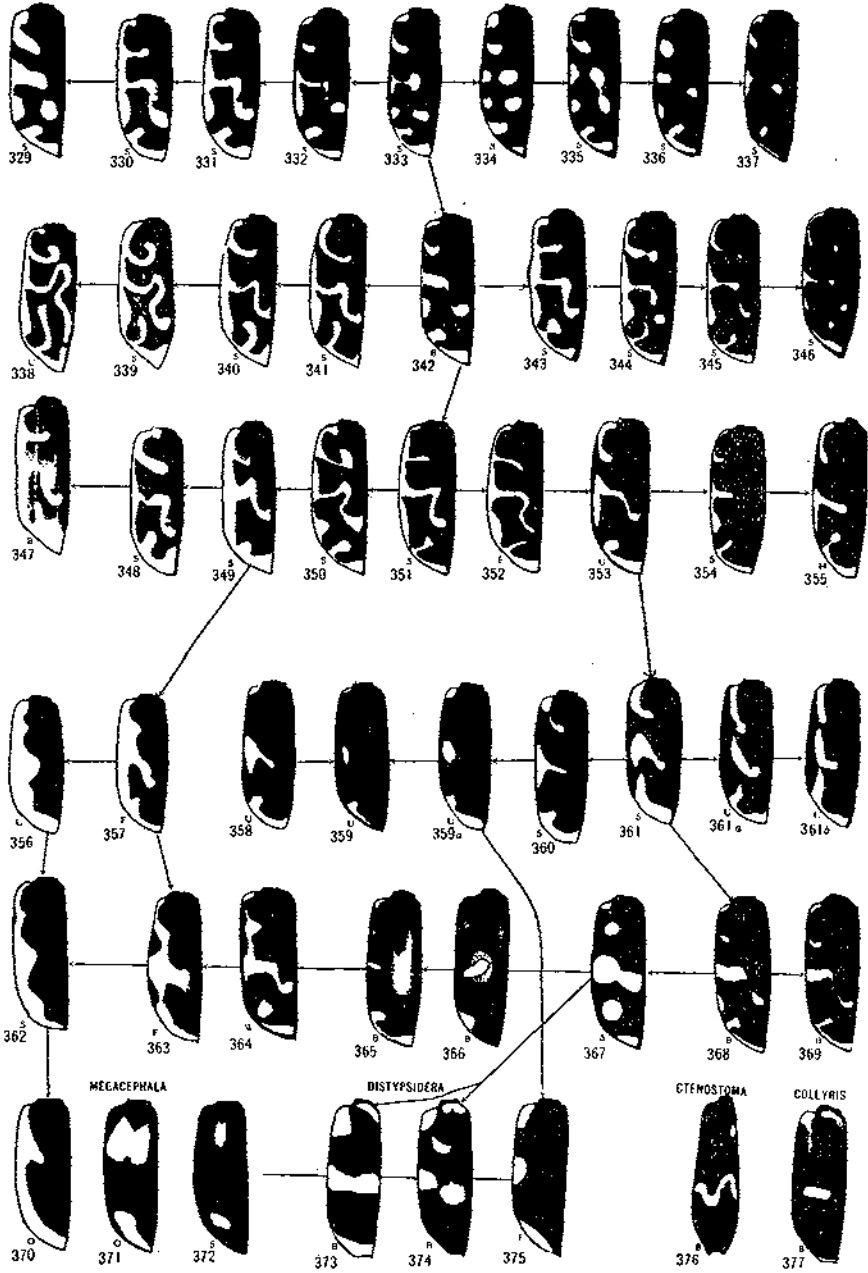
PLATE XV

## PLATE XVI

FIGURES 329-377. Showing the patterns of the principal Eurasian species exclusive of the *flexuosa* and *longipes-bivamosa-linosa* (Oriental) groups, with a few representative patterns from the genera *Megacephala*, *Distypsidera*, *Ctenostoma*, and *Collyris*. For meaning of letters see page 9. Figures 330-332 are related American species. Figures 329-355 show the typical and characteristic patterns of the genus *Cicindela* in which the portion of the elytron nearest the scutellum is without spots, in which bands 2 and 3 are fused and 5 and 6 are separate, and the modifications of the same.

## EXPLANATION OF PLATE

Fig. 329, *C. donegalensis* Klg. (Africa); 330, *hirticollis* Say (Illinois); 331, *repanda* Dej. (Illinois); 332, *12 guttata* Dej. (Illinois); 333, *lunulata* Fabr. (Europe); 334, *aphrodisia* Baudi (Cypris); 335, *lacrymosa* Dej. (Japan); 336, *10 guttata* Fabr. (Malay Arch.); 337, *discreta* Schm. (Malay Arch.); 338, *nitida* Wdm. (India); 339, *contorta* Fisch. (Europe); 340, *trisinata* Dej. (Europe); 341, *litterifera* Chd. (Europe); 342, *alboguttata* Klg. (Arabia); 343, *sumatrensis* Herbst (India); 344-345, *orientalis* Dej. (Europe); 346, *melancholica* Fabr. (Europe and Africa); 347, *3 signata* aber *subsuturalis* Souv. (Europe); 348, *circumdata* Dej. (Europe); 349, *circumdata* Dej. (Europe); 350, *angulata* Fabr. (India); 351, *sumatrensis* Herbst. (Oriental Region); 352, *despecata* Horn, after Horn (Madagascar); 353, *ancosisconensis* Harris (New York); 354, *funerea* subsp. *opigrapha* Dej. (New Guinea); 355, *variolosa* Blanch. (Salathy); 356, *galathea* Thiem. (Asia); 357, *lyoni* Vig., after Roske (Europe); 358, 359, 359a, *germanica* Linn. (Europe); 360, *atrata* Pall. (Europe and Asia); 361, 361a, b, *germanica* subsp. *obliquefasciata* Ad. (Europe); 362, *lacteola* Pall. (Asia); 363, *geminata* subsp. *potanini* Dok., after W. Horn (Tibet); 364, *purpurea* subsp. *limbalis* Klg. (Illinois); 365, *campestris*, showing an unusual light area—the stippled portions are dark areas with cuticula such as covers the lighter spots; 366, *ismenia* Gory—stippled areas as in 365; 367, *maura* Linn. (Europe); 368-369, *fischeri* Adams (Europe); 370, *Megacephala australasiae humeralis* McL. (N. W. Australia); 371, *quadrisignata* Dej. (N. Africa); 372, *M.* (*Styphloderma*) *asperata* Wat. (Africa); 373, *Distypsidera flavipes* McL. (Australia); 374, *D. gruti* Pasc. (Australia); 375, *Nickerlea distypsidroides* Horn, after Horn (Australia); 376, *Ctenostoma maculicorne* Chr. (Mexico); 377, *Collyris frushtoferi* Horn (Tonkin).



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PLATE XVI

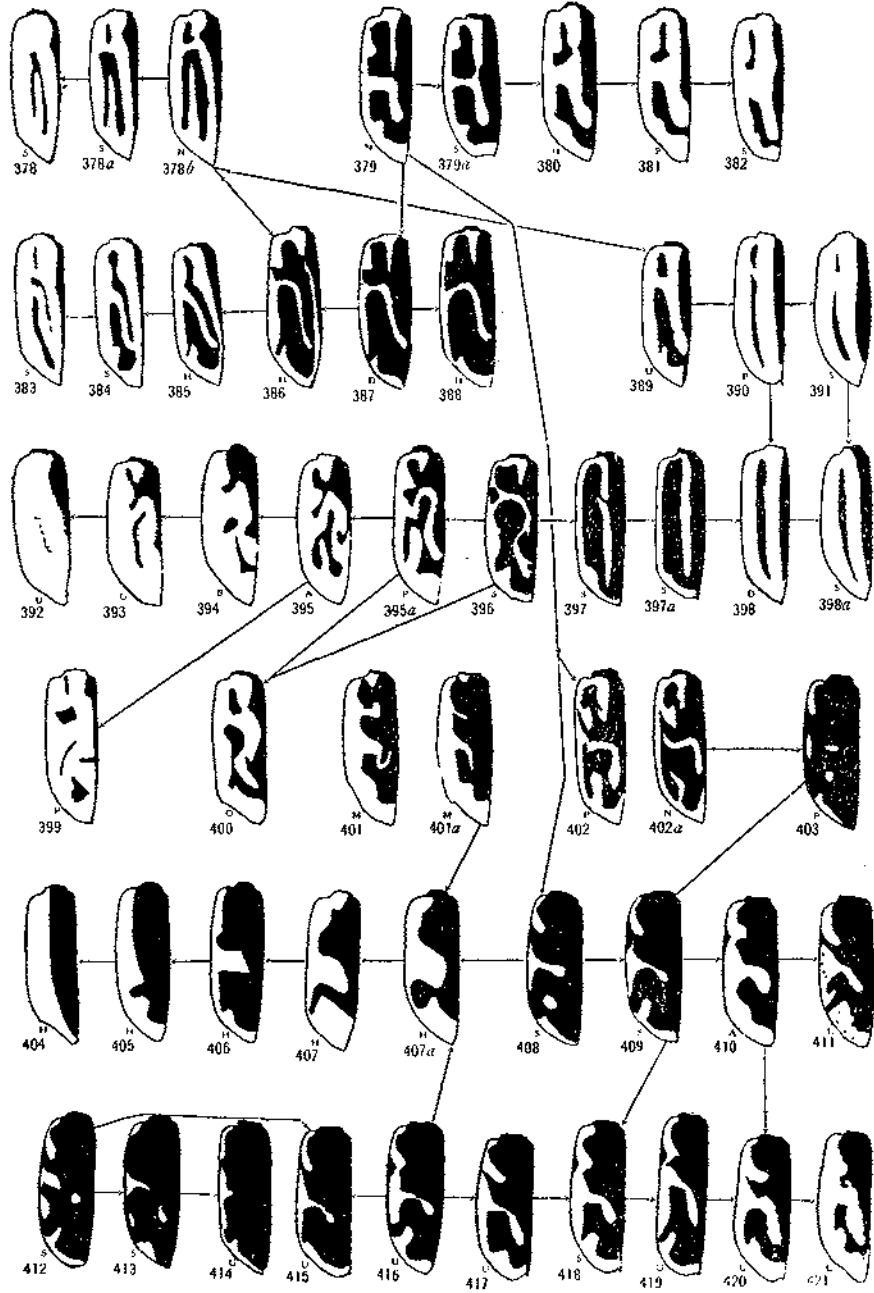


## PLATE XVII

FIGURES 378-421. Showing the patterns of the characteristic groups of species belonging to the Oriental and Australian Regions. For meaning of letters see page 9. They are in general of a character such as is commonly designated as specialized but show some unusual combinations of areas which tend to confirm the general interpretation here presented.

## EXPLANATION OF PLATE

Figs. 378-378a, b, c, *C. arancipes* Schm. (Borneo); 379-379a, *copulata* Schm. (India); 380, *anchoralis* subsp. *punctatissima* Schm. (China); 381-382, *ornata* Flt. (India); 383, 384, 385, *psammodroma* Chvr. (China); 386, 387, 388, *anchoralis* subsp. *punctatissima* Schm. (China); 389, *anchoralis* Chvr. (China); 390-391, *quadrilineata* subsp. *renei* Horn (India); 392-393, *ypsilon* Dej. (Australia); 394, *rafflesia* Chd. (Australia); 395-395a, *albicans* Chd. (Australia); 396, *longipes* Fabr. (Malay Islands); 397-397a, *l* *lineata* Fabr. (India); 398, 398a, *l* *lineata* subsp. *renei* Horn (India); 399, *singularis* Chd. (Nubia); 400, *longipes* Fabr. (Malay Islands); 401-401a, *wapleri* Lec. (Louisiana); 402-402a, *mucronata* Jord. (Malay Islands); 403, *pupilligera* Schm. (New Guinea); 404, *limbata* Schm. (India); 405, *maindroni* Horn (India); 406, *biramosa* Fabr. (India); 407, *bellana* Horn (India); 408, *funerata* subsp. *barbata* Horn (New Guinea); 409, *tuberculata* Fabr. (Australia); 410, *tuberculata* aber *latecincta* White (New Zealand); 411, *farryi* White (New Zealand); 412-413, *ro* *guttata* Fabr. (New Guinea); 414, *waltersi* McL. (Australia); 415, *feredayi* Bates (New Zealand); 418, *tuberculata* Fabr. (New Zealand); 419, *dunedensis* aber *wakefieldi* Bates (New Zealand); 420, *feredayi* Bates (New Zealand); 421, *perhispida* Brn. (New Zealand).



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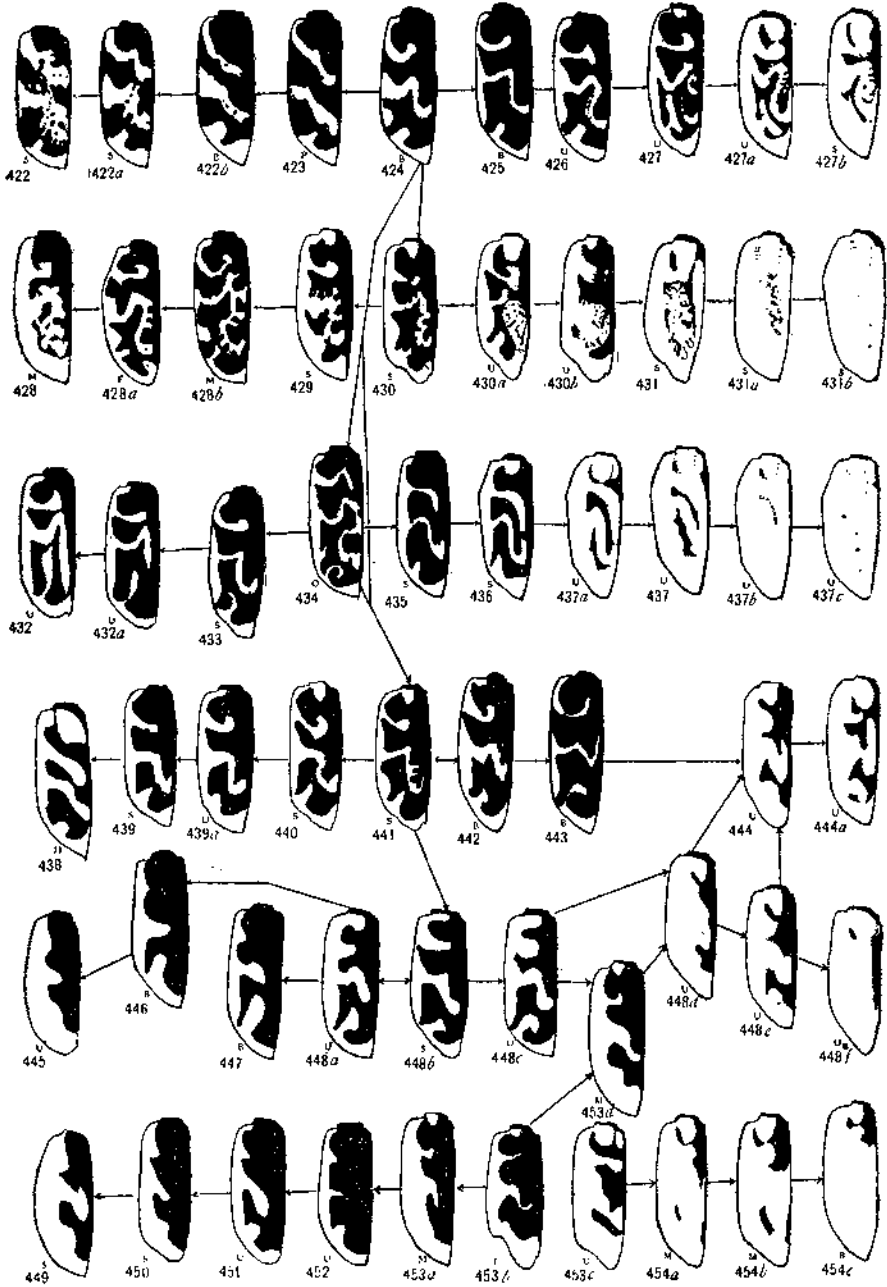
PLATE XVII

## PLATE XVIII

FIGURES 422-455. Showing the highly specialized patterns of the South American species belonging chiefly to the *cuprascens* and *argentata* groups of species. For meaning of letters see page 9. All the types have representatives in which pigment has almost entirely disappeared as a rule and there is a strong tendency for the area of the media trachea to degenerate along with the reduction of that trachea (see figures 16 and 20).

## EXPLANATION OF PLATE

Figs. 422-422a, b, *C. apiata* Dej. (S. A.); 423, *apiata* aber *claussemi* Putz. (S. A.); 424, *gormazi* Reed. (Chili); 425, *mixta* Horn (Ecuador); 426, *trifasciata* Fabr. (S. A.); 427-427a, b, *graphiptera* Dej. (S. A.); 428-428a, after Chevrolot 428b, *patagonica* subsp. *cherubim* Chvr. (S. A.); 430-430a, b, *marginata* Fabr. (Texas); 431-431a, b, *nivea* Kirby (S. A.); 430-432a, *gabbi* G. Horn (California); 433, *trisignata* Dej. (Asia); 434, unidentified species from Arica, Peru, in the Oxford University Museum; 435, *curvata* Chvr. (Mexico); 436, *dorsalis* aber *sauleyi* Guer. (Texas); 437-437a, b, c, *dorsalis* Say (Mass.); 438, *malaris* Horn (Pebas, Amazons); 439-439a, *nevadica* var. *knausi* Leng (Kansas); 440, *cuprascens* Lec. (Illinois); 441 *hamata* Brill. (Mexico); 442, *chloroccephala* Chv. (Vera Cruz, Mex.); 443, *leucohoe* Bat. (Mexico); 444, *macronema* Chd. (Mexico); 445, *togata* Laf. (Texas); 446, *auraria* Klg. (S. A.); 447, *boops* (West Indies); 448, *macronema* Chd. (Mexico); 449, *pamphila* Lec. (Texas); 450, *togata* Lec. (Texas); 451, *californica practexta* Lec. (Texas); 452, *marginata* Fabr. (Texas); 453a, b, c, d, *wapleri* Lec. (Louisiana).

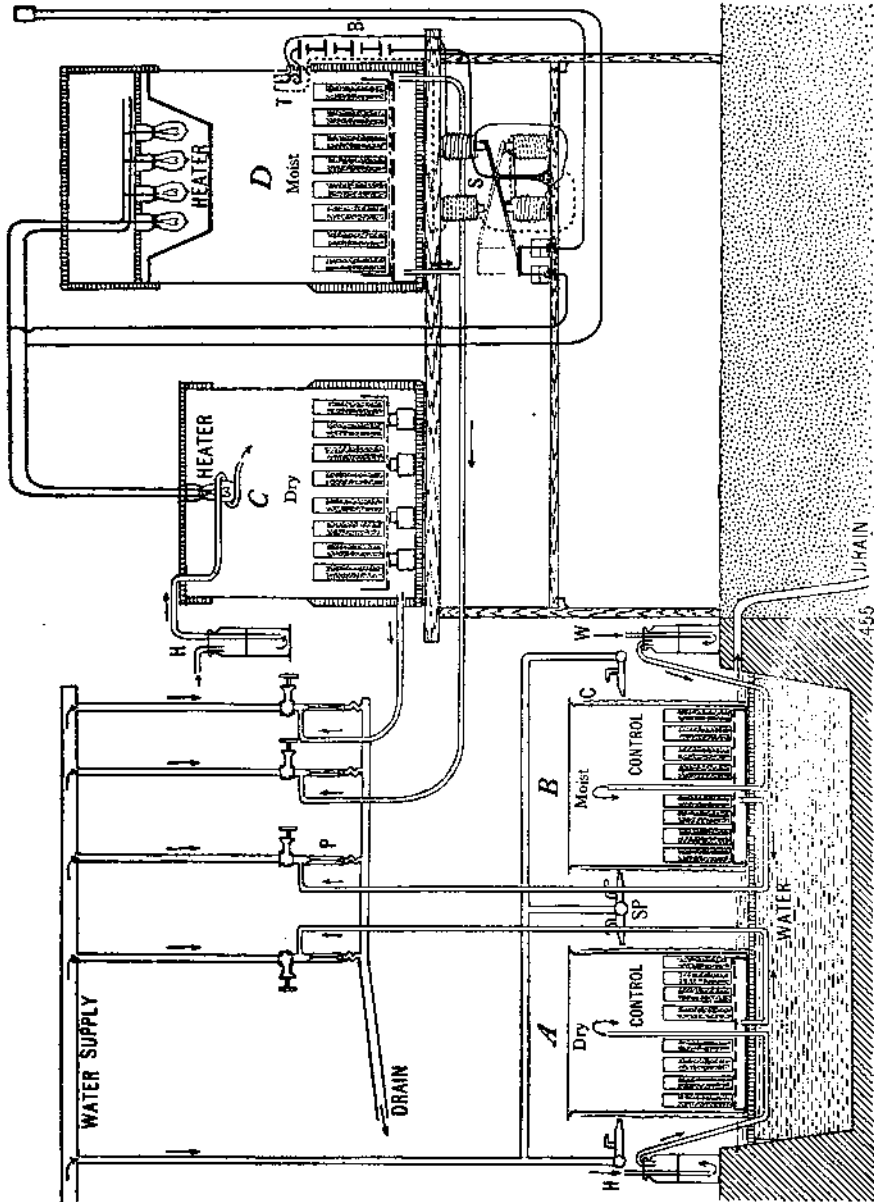


## PLATE XIX

## EXPLANATION OF PLATE

FIGURE 455. Showing the equipment used in the experiments on modification of tiger beetle color and color patterns.

The experiments were conducted in four chambers; two, A and B, which were of galvanized iron, rested with their bottoms in a concrete tank of running water. They were wrapped with cheese cloth and sprayed with jets of water on two sides which kept the mean temperature at 21° C. throughout the summer. The other two, C and D, were heated from above with electric lights, blackened in C and separated from the main chamber by a copper jacket in D. These were heated to a point 10° C. above the temperature of the greenhouse except during the middle of the day. The switch shut off the heat at about 35° C. air temperature and the sun continued to heat the chamber so that the maximum soil temperature sometimes reached 40° C. or more by midafternoon. Air was drawn through the tanks by filter pumps and, in the case of the control tanks, through sulfuric acid for the dry one and water for the moist one, but this intake was not maintained for the high temperature tanks at all times because of mechanical difficulties. The moisture in the moist chambers was maintained by frequent additions of water to the soil, while in the dry chambers as little water as possible was added. *H*, sulphuric acid bottles; *S*, mercury switch; *T*, thermostat; *B*, batteries; *W*, water bottles; *SP*, spray nozzles; *C*, cloth cover.

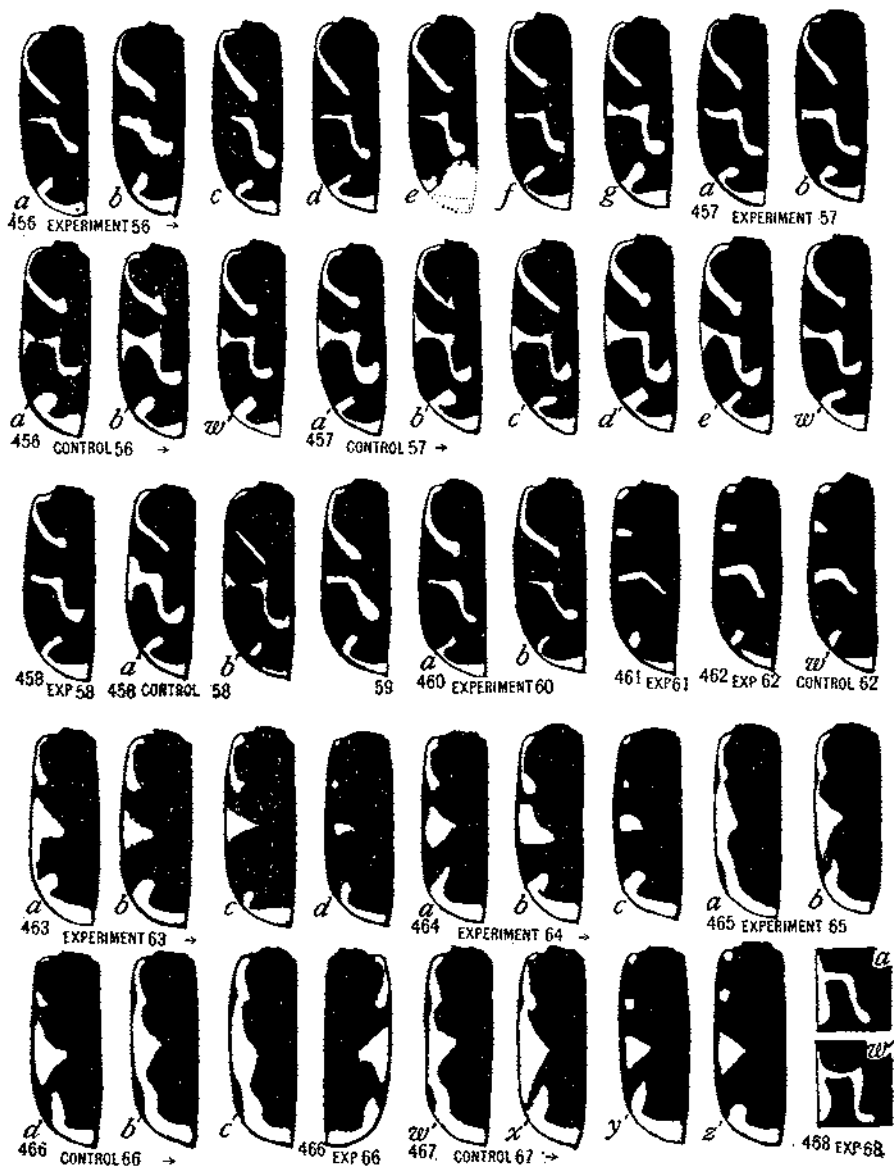


## PLATE XX

FIGURES 456-465. Showing the color patterns of specimens of *C. tranquebarica* Herbst., *C. purpurea limbalis* Klg., and *C. scutellaris lecontei* Hald. subjected to high temperature under moist and dry conditions and placed in an ice box during their prepupal and pupal life. With them are shown controls which were kept at normal temperatures or lower and designated with letters *a'*, *b'*, etc., and a few collected from the normal habitat from the same generation, designated *w'*.

## EXPLANATION OF PLATE

Fig. 456*a-g*, the elytra of seven specimens of *C. tranquebarica* which passed the late larval, prepupal, and pupal stages in a warm moist chamber; mean temperature of the soil, 37° C.; maximum for the warmest week, 40° C.; control, 456*a'*, *b'*, *w'*, at 21° (Experiment 56); 457*a-b*, the elytra of two specimens of *C. tranquebarica*, which passed the late larval, prepupal, and pupal stages in a warm dry chamber, mean temperature 40° C.; control, 457*a'-e'-w'* at 21° C. (Experiment 57); 458, the same as 457 but dry instead of moist; 458*a'-b'* control of the same (Experiment 58); 461, the same moist warm treatment as described under 456 applied to *C. purpurea limbalis*; 462, the same as 461 but dry instead of moist; for normal patterns see figure 512, plate XXVIII; a collected specimen from the same generation showing the extreme type of cross band reduction and forward curvature found either in the controls or the collections from the habitata; 459, showing the pattern of a specimen of *C. tranquebarica* which was forced through its transformations in the fall by a temperature of 37° C. beginning October 1, so that there was no hibernation. This specimen was one emerged early in December. The others emerged in June but none of them showed any modification; 460*a-b*, the same treatment as 456 but dry instead of moist (Experiment 60); 463, showing the patterns of specimens of *C. scutellaris lecontei* Hald. subjected to conditions similar to those mentioned for figure 456; 463*d* shows markings reduced below anything ever collected near Chicago or produced in the controls (Experiment 63); 464*a, b, c*, showing the patterns of elytra of *C. scutellaris lecontei* subjected to mean temperature of 39° C. under very moist conditions (Experiment 64); 465*a, b, c*, showing the elytral patterns of two specimens of *C. scutellaris lecontei* Hald. kept in an ice box during the pupal and prepupal stages; 10 to 12° C. from July 29 to September 3; 16 to 20° September 3 to October 16; 466 shows the elytron of a specimen kept at a mean temperature of 40° C., moist; 466*a', b', c'* are the control of the same kept at 21° C.; 467*w', x', y', z'* show elytra of specimens collected in the habitat from which the experimental material came, selected to show the range of variation; 468*a* and *w' . . a* shows the middle band of a specimen of *C. hirticollis* showing the rounded angle, transverse portion perpendicular to the inner border of the elytron and the hooked portion at the end rounded—compare with the normal shown in 468*w'*.





## PLATE XXI

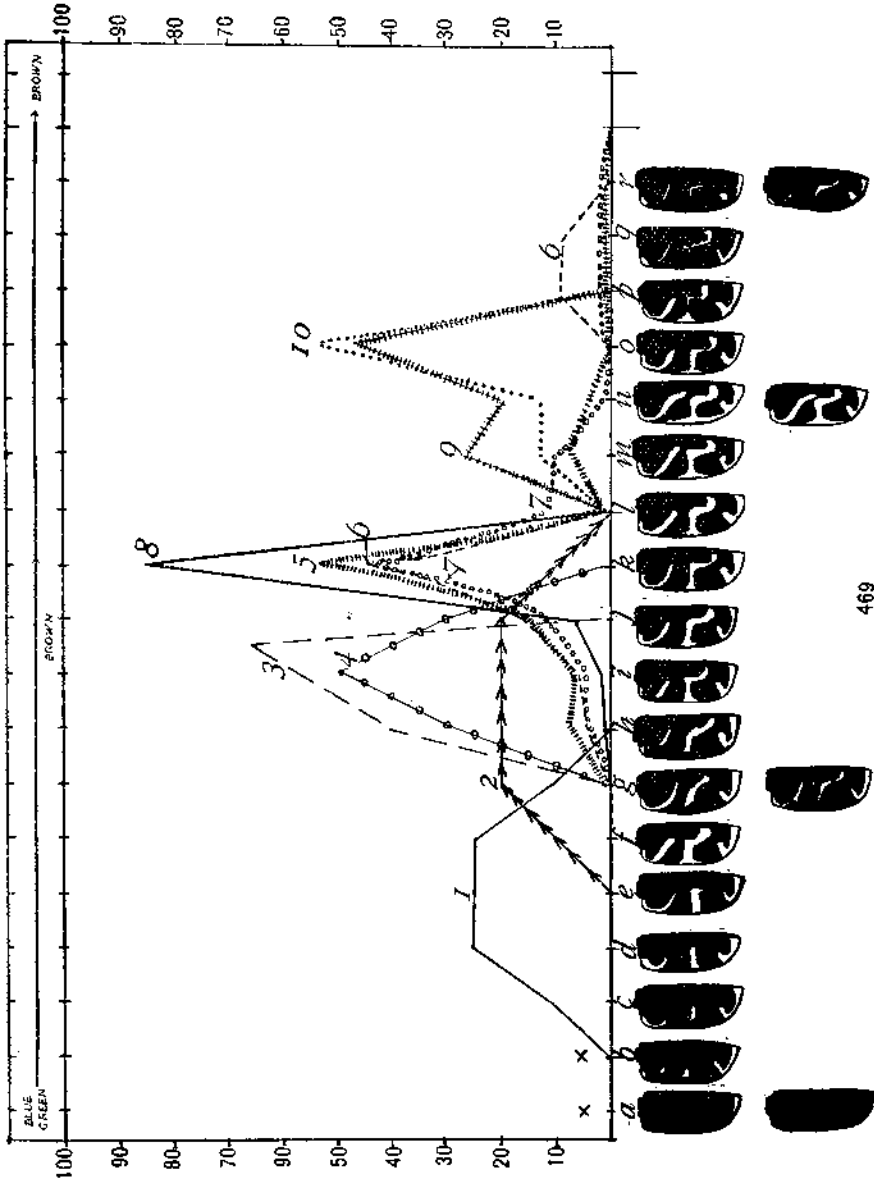
## EXPLANATION OF PLATE

FIGURE 469. Showing the range of variation in the group of races included under the name *tranquebarica* Herbst. The classes of patterns are arranged in a series *a, b, c, d, e, f*, etc., from left to right and the percentage of individuals in each class for several localities is graphically represented. At the top is indicated the color of the elytra to which the patterns belong but these do not fall in the same classes as the patterns. The graphs are numbered and the localities which they represent are numbered on figure 469a.

The graphs are for the following localities, approximate, altitude, etc.

No.	Locality	Altitude	No. Specimens	Vegetation and Climate
1.	Las Vegas, Nev.	2020 ft.	8	Desert
2.	Provo, Utah	4500 ft.	15	"
3.	San Bernardino, Cal.	1060 ft.	10	Semi desert
4.	Hagerman, Idaho	2600 ft.	5	" "
5.	Galveston, Tex. (vicinity)	100+ ft.	130	Savanna
6.	Dodge City, Kan.	2500 ft.	69	Steppe
7.	Fayetteville, Ark.	1500 ft.	42	Deciduous forest
8.	Framingham, Mass.	200 ft.	149	" "
9.	Aweme, Manitoba	1180 ft.	73	Steppe
10.	Alamosa, Colorado	7536 ft.	7	"

The classes into which they are divided are somewhat artificial and some of the curves are divided.



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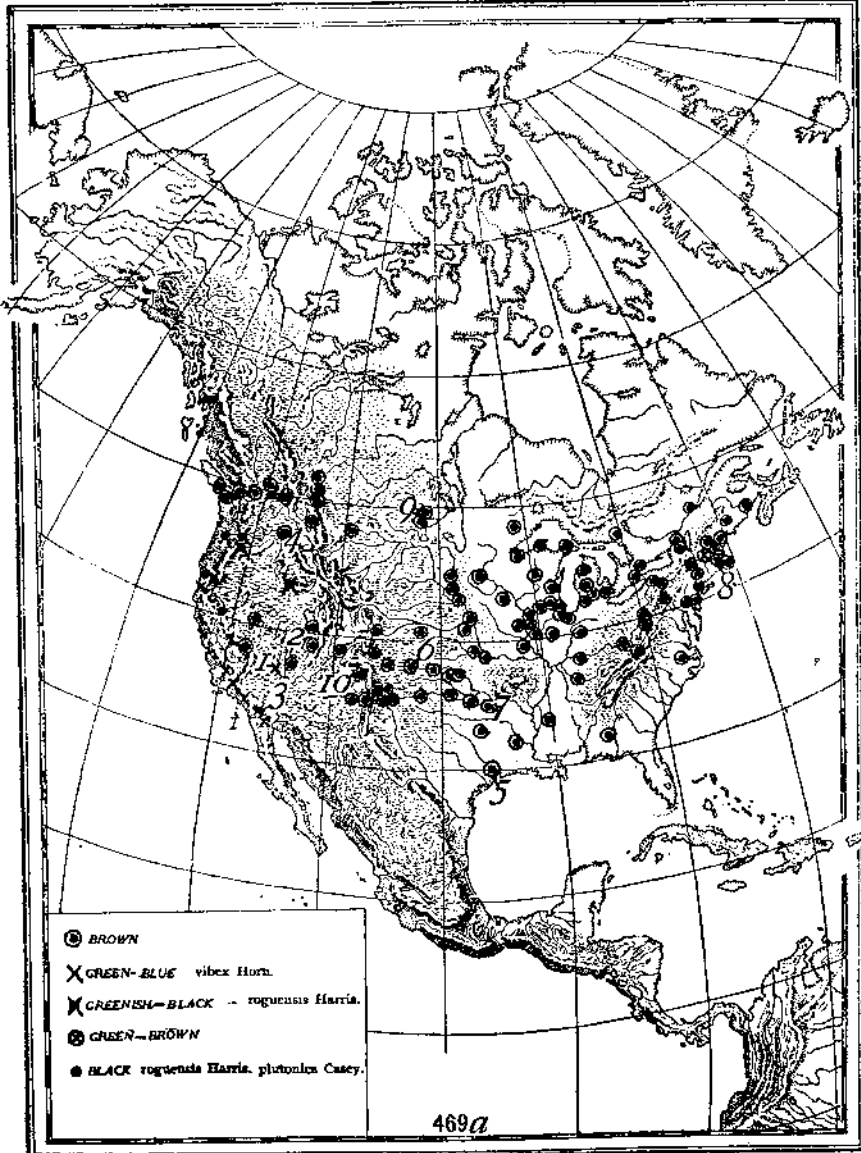
COLORS OF TIGER BEETLES

PLATE XXI

## PLATE XXII

## EXPLANATION OF PLATE

FIGURE 469a. Showing the distribution of *C. tranquebarica* in N. America. The numbers refer to the graphs shown in figure 469. The legend shows the elytral color.

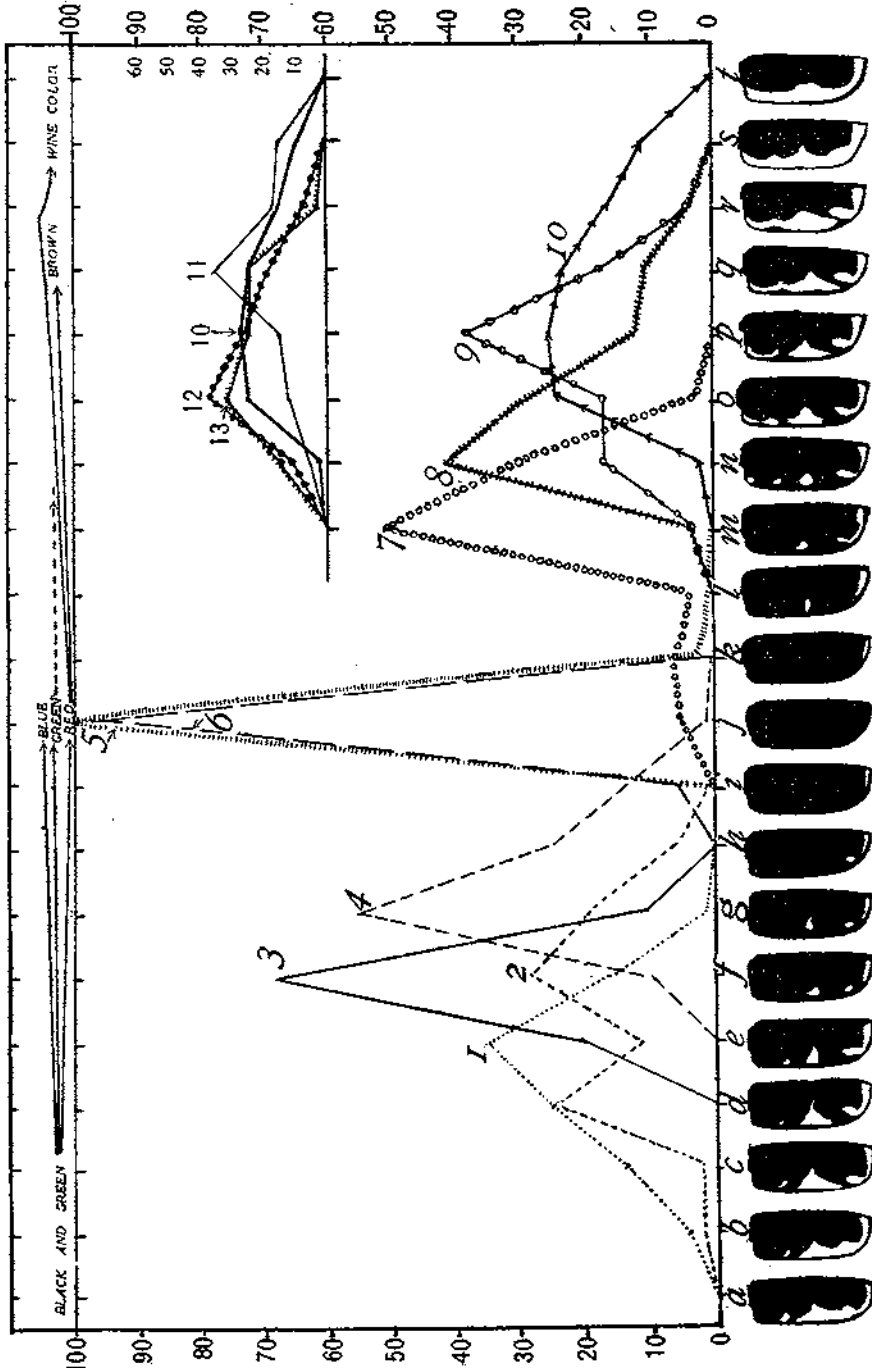


## PLATE XXIII

## EXPLANATION OF PLATE

FIGURE 470. Showing the range of variation in the group of races included under *C. scutellaris* Say. General plan as in figure 469, plate XXI. Here the individuals are arranged into classes which are strictly geographic; beginning in Massachusetts at the extreme left, they are arranged as encountered as one passes southward along the Atlantic coast and westward through the Gulf States. From Dallas, Texas, classes are arranged in order as one passes northward through western Oklahoma, Kansas, Nebraska, and South Dakota and then eastward through the Great Lakes. The classes on the extreme right (*s* and *t*) are from Aweme, Manitoba.

Locality	No. Specimens	Generation	Collector	Altitude	Climate or Vegetation
1. Framingham, Mass.	51	1902-1904	A. C. Frost	220 ft.	Deciduous Forest
2. Providence, R. I.	85	1902	Bert Nock	50 ft.	" "
3. Aqueduct, N. Y.	98	1903	L. H. Joutel	50 ft.	" "
4. Raleigh, N. C.	59	1904	C. S. Brimley	320 ft.	" "
5. Mobile, Ala.	20	1911	V. E. Shelford	50 ft.	" "
6. Medora, Kan.	150	1904	"	1600 ft.	Steppe
7. Topeka, Kan.	150	1904	"	900 ft.	Savanna
8. Elma, Iowa	30	1902-1904	Rev. J. C. Warren	1000 ft.	"
9. Starved Rock (Utica), Ill.	40	1905-1906	V. E. Shelford	470 ft.	"
10. Miller, Ind.	200	1904-1905	"	600 ft.	Deciduous Forest
t. Aweme, Man.			N. Criddle	1180 ft.	Steppe



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COLORS OF TIGER BEETLES

PLATE XXIII

## PLATE XXIV

## EXPLANATION OF PLATE

FIGURE 470a. Showing the distribution of the group of races included under *C. scutellaris* Say. The legend indicates the color of the elytron. The numbers (*italics*) refer to the classes of color patterns indicated in figure 470, plate XXIII. The lines and numbers indicate mean annual rainfall in inches. The mean annual rainfall to the left or west of the line designated as 20 is less than 20 inches, to the right or east more than 20 inches. To the east and south of the line designated as 30 the mean annual rainfall is more than 30 inches. To the east and south of the line designated as 40 it is more than 40 inches. Note that the colors are fairly well correlated with rainfall.



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COLORS OF TIGER BEETLES

PLATE XXIV



## PLATE XXV

## EXPLANATION OF PLATE

FIGURE 471. Showing the range of variation in the group of races falling under *C. purpurea* Oliv. General plan of arrangement as in the preceding charts on other species (Pls. XXI and XXIII). In the case of this species the immaculated elytroned types which are very rare in occurrence are taken as a central type. Those to left are level ground inhabitants in which the reduction of patterns is characterized by a withdrawal of the middle band from the elytral margin. Those to the right are the steep clay bank inhabitants, except possibly class "f" (*C. decemnotata* Say); classes *a, b, c, C. cimarrona* Lec.; *d-h, C. purpurea* Oliv., *graminea* Schpp., *audoboni* Lec., *spreti* Lec. Those to the right are *splendida*, Hentz, *transversa* Leng, *denverensis* Cas., *limbalis* Klg. The graphs are for the following localities with approximate altitudes, vegetation, etc.

Locality	No. Specimens	Color or Race	Altitude	Climate or Vegetation
1. Fort Collins, Colo.	7	Green and black	5600 ft.	Steppe
2. Framingham, Mass.	128	Winecolor, brown, some greenish	100 ft.	Deciduous Forest
3. Puget Sound, Wash.	7	Green	10 ft.	Conifer
4. Kimmich, Mo.	29	<i>transversa</i>	425 ft.	Deciduous Forest
5. Topeka, Kan.	100	<i>splendida</i>	900 ft.	Savanna
6. Glencoe, Ill.	54	<i>limbalis</i>	600 ft.	"
7. Aweme, Man.	10	"	1080 ft.	Steppe
8. Sedalia, Colo.	....	Red Classes, p-s	5800 ft.	"



## PLATE XXVI

## EXPLANATION OF PLATE

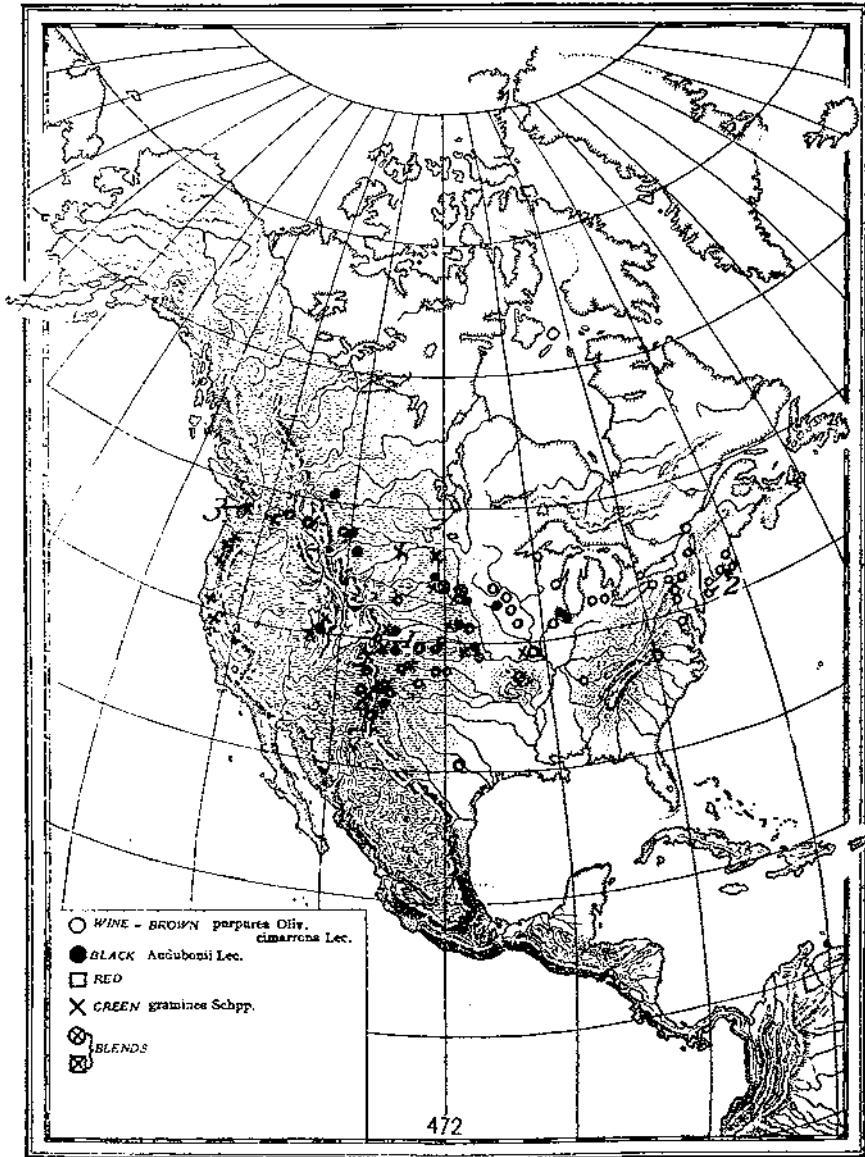
FIGURE 471a. Showing the distribution of the *limbalis*, *denverensis*, *transversa*, and *10 notata* races of *C. purpurea* with numbers referring to the graphs in figure 471, plate XXV, and legend showing colors.



## PLATE XXVII

## EXPLANATION OF PLATE

FIGURE 472. Showing the distribution of the *purpurea*, *graminea*, *audobonii*, and *cimarrona* races of *C. purpurea* with numbers referring to the graphs on figure 471, plate XXV, and legend showing colors.

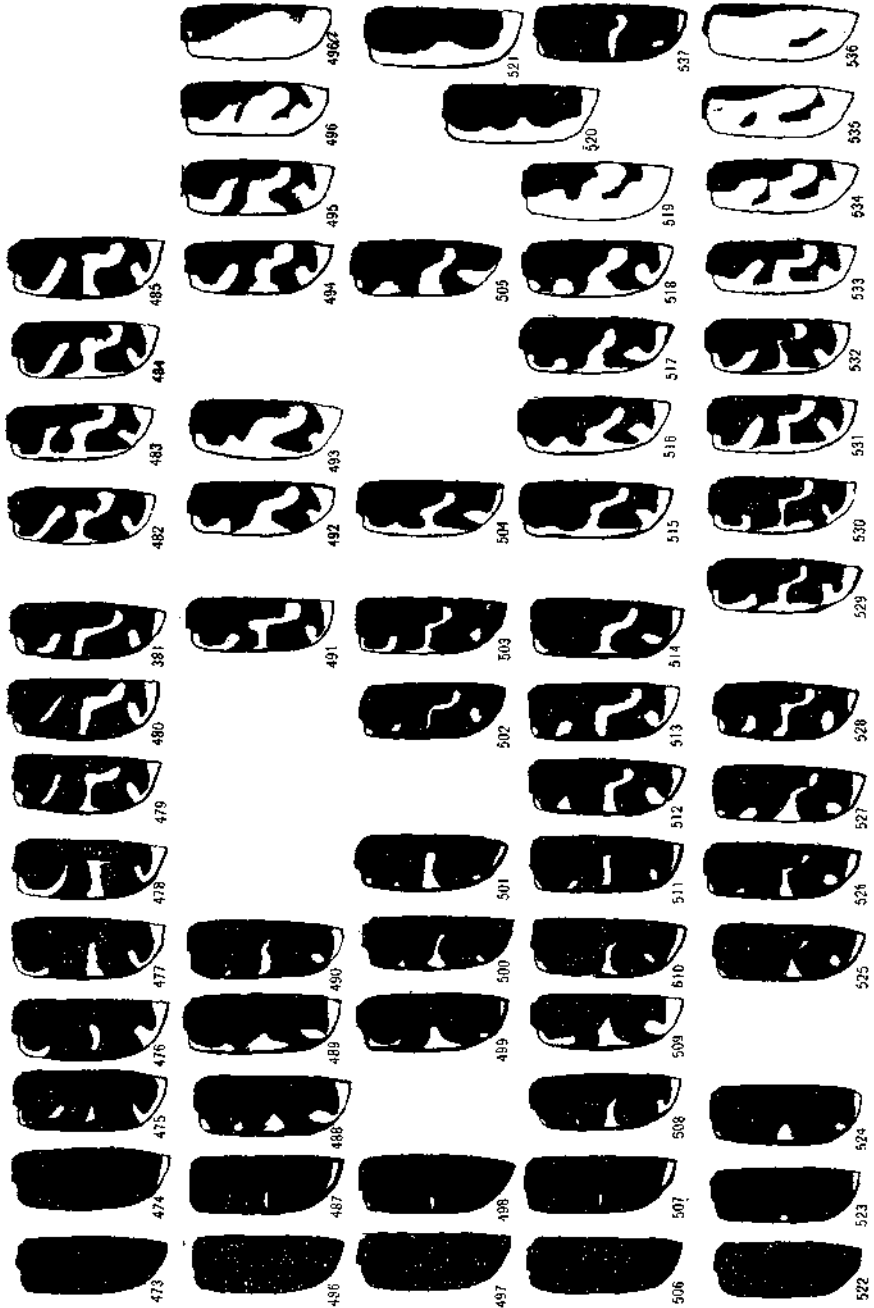


## PLATE XXVIII

Showing the parallelism of patterns of the north stem of *W. Horn's* phylogeny, and *C. sexguttata* Fabr. Compare the rows with one another.

## EXPLANATION OF PLATE

Figs. 473-474, *tranquebarica* Herbst subsp. *plutonica* Cas. (California) drawn from descriptions by Leng; 475-478, do. subsp. *vibex* Horn (Las Vegas, Nev.); 479, do. (San Bernardino, Cal.); 480, greenish brown form of *tranquebarica* (Hagerman, Idaho) (*roguensis* Harris); 481, *tenuicincta* Sch. (Salt Lake); 482, *tranquebarica* (Framingham, Mass); 483, *tenuicincta* Schpp. (Saltair, Utah); 484, *tranquebarica* Herbst (Alamosa, Colo.); 485, do. (Las Vegas, Nev.); 486-490, *scutellaris* Say, varieties—see figure 468 and description; 491, *echo* Cas. (Great Salt Lake); 492, *willistoni* Lec. (Lake Como, Wyo.); 492, *fulgida* Say (Kansas); 494-496, *latesignata* Lec. (San Diego, Cal.); 497-501, *pulchra* Say (499-501—Alpine, Texas, drawing supplied by Prof. H. F. Wickham, from specimens in his collection); 502, *latesignata* aber. *tenuicincta* Blaisdell (Saltair, Utah); 503-505, *longilabris* Say, varieties; 504-505, (N. Mexico); 506-518, *purpurea* Oliv., varieties (see Fig. 470); 508-509, 516-518 (Sedalia, Colo.); 519, *generosa* subsp. *mantoba* Leng.; 522-523, *sexguttata* (Onaga, Kansas); 524, do. (Chicago); 525-526, do. (Woods Holl.); 527, *sexguttata* subsp. *patruela* Dej. (Lakehurst, N. J.); 528, 12 *guttata* Dej. (Chicago); 529, *ancosisconensis* Harris; 530, *repanda* Dej. (Chicago); 531-532, *generosa* Dej.; 531, do. (Framingham, Mass.); 532, do. (Lakehurst, N. J.); 533-534, *venusta* Lec. (Aweme, Man.); 535-536, *limbata* Say (Aweme, Man.); 536, *purpurea*, showing reduced and shortened marking.



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COLORS OF TIGER BEETLES

PLATE XXVIII



## PLATE XXIX

Showing Development and General Modification of Colors in Experiments in  
*C. scutellaris lecontei* Hald.

## EXPLANATION OF PLATE

- Figs. 538-542. Development of color in the ventral side.
- 538. 4 hours after emergence.
  - 539. 10 hours after emergence.
  - 540. 11 hours after emergence.
  - 541. 15 hours after emergence—adult coloration.
  - 542. Adult coloration in a dark individual.
- Figs. 543-549. Color development and color changes in an individual of *C. lecontei*.
- 543. 1 hour after emergence.
  - 544. 11 hours after emergence.
  - 545. 13 hours after emergence; compare with 553.
  - 546. 15 hours after emergence.
  - 547. 3 to 15 days after emergence; drawn at end of third day.
  - 548. 42 days after emergence.
  - 549. 85 days after emergence.
  - 550. *C. lecontei*, color of modal class, Miller, Ind., April, 1906.
  - 551. *C. lecontei*, Miller, Ind., June, 1906.
  - 552. *C. lecontei*, color of modal class, Miller, Ind., April, 1905.
  - 553. *C. scutellaris rugifrons*, typical specimen, Raleigh, N. C.
  - 554. *C. scutellaris*, typical specimen, Topeka, Kansas (not modal class).
  - 555. *C. lecontei*, larvae subjected to hot dry conditions during prepupal and pupal stages, note reduced markings and color—compare with normal ontogeny series above (Experiment 63); mean temperature 37°; dry; compare with 554 and 553.
  - 556. *C. lecontei*, larvae forced by high temperature and brought through without hibernation (Experiment 59a; mean temperature 37° C.; moist.
  - 557. *C. lecontei* modified by cold conditions during the pupal stage; (Experiment 65); mean temperature, 12° C.; moist. Note dull color and peculiarities of markings.
  - 558. Peculiar individual from Starved Rock (Utica), Ill., showing the tendency for all the highly colored species to produce purple forms occasionally. This type occurs at Utica on the coarse sands.



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## PLATE XXX

Showing Color Development and General Modification in Experiments on Species Named.

EXPLANATION OF PLATE

- Figs. 559-562. Color development in *Cicindela hirticollis*.  
 559. Condition 4 hours after emergence.  
 560. Condition 15 hours after emergence.  
 561. Condition 21 hours after emergence.  
 562. Condition 21 days after emergence, full adult color.
- Figs. 563-565. Color development in *C. purpurea*.  
 563. Condition 20 hours after emergence.  
 564. Condition 4 days after emergence.  
 565. The same specimen as in figure 6, killed and dried on the fourth day after emergence.
- Figs. 565-570. Experimental modification of color and color pattern by conditions during the prepupal and pupal stages.
566. Dwarfed specimen of *C. hirticollis* produced by forcing the larvae without hibernation in their last winter (Experiment 70); mean temperature, 37° C.; moist.
567. Normal individual of *C. tranquebarica*, collected in the field.
568. Specimen with color modified by being kept in an ice box, during the pupal stage, like variety in eastern mountains (Experiment 65a); mean temperature, 12° C.; moist.
569. Specimen with both pattern and color modified by hot dry conditions (Experiment 60); mean temperature, 37° C.; dry. Like variety in the western states.
570. Specimen with both pattern and color modified by hot wet conditions, like variety in the moist southern states (Experiment 56); 37° C.; moist.

PLATE XXX



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## PLATE XXXI

Showing Color Development and General Modification in Experiments on *C. purpurea* subsp. *limbalis*.

EXPLANATION OF PLATE

Figs. 571-574. Color development in *C. purpurea* subsp. *limbalis*.

571. Condition at emergence.
572. Condition 12 hours after emergence.
573. Condition 34 hours after emergence.
574. Condition 15 days after emergence.
575. Normal collected individual.
576. Specimen killed and dried when at stage shown in figure 573.
577. Experimentally modified individual, in hot dry conditions during prepupal and pupal stages. Resembles specimens from eastern Kansas.
578. Specimen with color modified by being kept in an ice box during the pupal stage (Experiment 65*b*); mean temperature, 12° C.; moist.
579. Specimen modified by hot moist conditions during the prepupal and pupal stage (Experiment 61); mean temperature, 37° C.; moist.

PLATE XXXI



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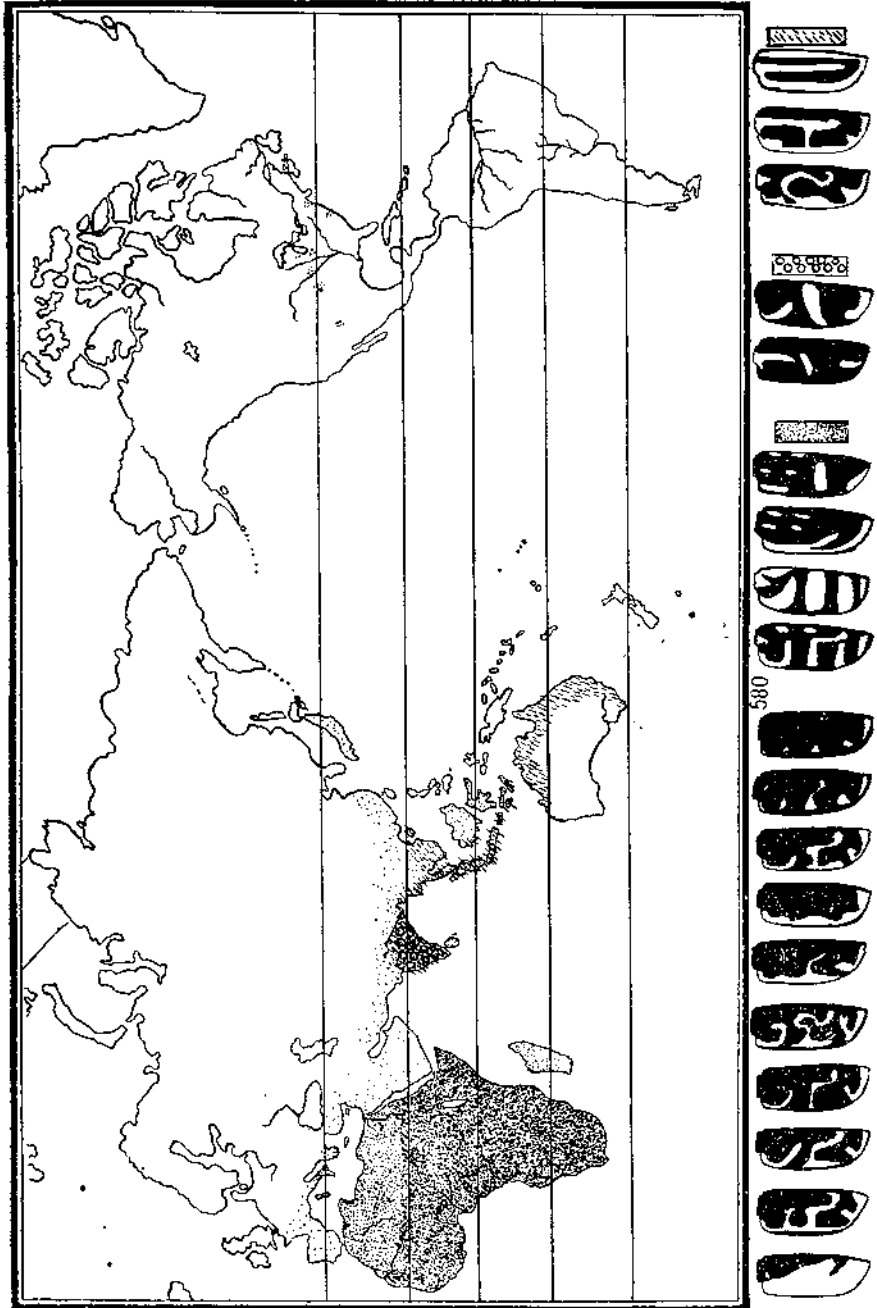
579



## PLATE XXXII

## EXPLANATION OF PLATE

FIGURE 580. Showing the geographic distribution of types and patterns. The first series at the left are world-wide in distribution, being most generalized in Eurasia and North America. The second group of patterns belong to several groups of species but all are characterized by the presence of three spots at the base and along the elytral suture. They are most numerous in Africa and India. The next group shows the relatively rare type with the pattern oblique but in the opposite direction from the slope of the tip of the elytron. The last type is one showing peculiar joinings of markings characteristic of species found chiefly in Indo-Australian region.



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COLORS OF TIGER BEETLES

PLATE XXXII