Studies on the Color Patterns in Crosses of *Tropisternus* from Western Mexico with Other Color Forms of the *Tropisternus collaris* Complex (Coleoptera: Hydrophilidae)¹

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In a previous paper (3), I referred all of the North American forms of Tropisternus (s. str.), except T. niger d'Orchymont, to Tropisternus collaris (Fabricius). The close relationship of the North and South American color forms is evident, but the genetic evidence of F_1 and backcross incompatibility between geographically separated populations is now more extensive and indicates the existence of partial sterility barriers between several of the populations. Detailed data are presented in the companion paper by B. Dancis (1). The critical experiments with the hybridization of mexicanus-like forms from Panama and other parts of Central America have not yet been made, however, and until the relationship of the South American populations of collaris with the geographically adjacent populations of mexicanus-like forms can be determined, I think that we should retain the present arrangement and consider all the color forms as belonging to the Tropisternus collaris Complex. The known color forms of this group are shown in semi-diagrammatic figures and a rough indication of their distribution is given in Plate I, figs. 1-13.

In western Mexico (Sinaloa, Nayarit, and Jalisco) very lightly pigmented forms of *T. collaris* are common. In a collection from Culiacan, Sinaloa (in California Academy of Science), the pattern is so reduced in some specimens that the pronotal blotch is represented by a fine dark line and the elytral dark lines are greatly reduced and fragmented (2). The reduction of the dark markings seems to be greatest in the central coastal area of Sinaloa, and specimens from Nayarit and Jalisco, although still showing reduced patterns, are closer to typical mexicanus (Castelnau) from eastern Mexico and Central America. Sufficient collecting has not been done in central Mexico to prove the geographical continuity or discontinuity of these western populations with typical mexicanus, but it seems probable that we are here dealing with an isolated population adapted to more extreme desert conditions than the eastern and southern populations.

Collections were made in June, 1965, in Sinaloa and Nayarit, and living beetles were transported to the laboratory in Bloomington. None of the wild specimens nor specimens reared from them showed color patterns which rated less than 7 on the head, 21 on pronotum, or 30 on elytra by the scale (Pl. II) used in previous work (2). Specimens used in crosses reported here were from the Rio Presidio, near towns of Walamo, Sinaloa (WAL), or Villa Union (VUN).

Crosses of individuals from the Rio Presidio population were made with laboratory stocks of *striolatus* (LeConte) from the White River

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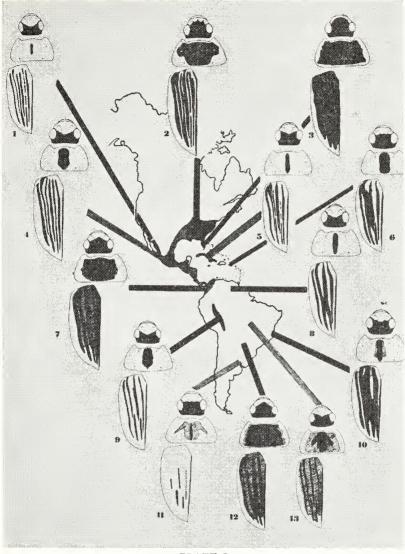
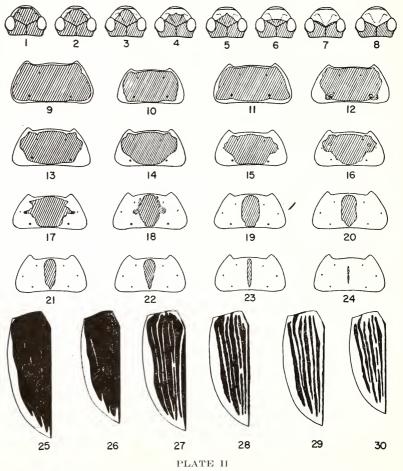


PLATE I

Semi-diagrammatic figures representing the color patterns of the known members of the *Tropisternus collaris* Complex with approximate indications of their distribution: 1. Light form of *mexicanus* (Castelnau) from Sinaloa, Nayarit, and Jalisco, Mexico 2. striolatus (LeConte) eastern United States 3. viridis Young and Spangler, Florida and southern Georgia and Alabama 4. Typical form of *mexicanus*, central United States, Mexico, and Central America 5. proximus Sharp, Cuba 6. Puerto Rican form of collaris (Fabricius) 7. Melanic form of collaris from Colombia 8. Typical form ? of collaris from Venezuela and northeastern Brazil 9. Form of collaris from dalong western edge of Amazon region in Bolivia and Peru 10. Form of collaris from Sao Paulo region of Brazil 11. lepidus (Castelnau), Argentina 12. parananus Sharp, Parana region of Brazil 13. Melanic form of collaris from Matto Grosso of Brazil. near Elnora, Indiana (*WHR*), viridis Young and Spangler from Bivin's Arm of Payne Prairie near Gainesville, Florida (*BIV*), and a melanic form of *collaris* from Lago de Ayapel, Colombia (*AYA*). The color patterns found in the results of these hybrid crosses, F_1 crosses, back-crosses to the recessive parent type, and crosses with other stocks are tabulated in Figs. 15-24.



Semidiagrammatic figures of head, pronotal, and elytral patterns of United States forms of *Tropisternus collaris* complex and intermediates between them. Numbers on histograms in figures 14-24 refer to numbers of patterns on this plate. (After Young, 1961.)

A number of other crosses were made using specimens from the Rio Piaxtla near town of San Ignacio, Sinaloa, and from ponds and a stream near San Blas, Nayarit. Most of these either produced small numbers of offspring or the results were similar to those with the Rio Presidio individuals. Most of the crosses made were of wild Walamo males to laboratory stock females, but crosses using wild Walamo females and laboratory males were more successful and did not show any apparent differences as far as the color pattern is concerned.

Although the results of these crosses are not as clear cut as could be desired, they do show the presence of a switch mechanism and suggest some interesting relationships between the color forms. The wild population from which the lightly pigmented *mexicanus* parents were drawn is quite uniform as shown in Fig. 14. There is some variation, but most is of such a minor nature it is difficult to assay. The pronotal blotch in some specimens shows a reduction at the posterior end, but this did not reappear in hybrids or backcrosses and so is considered to be due to developmental factors. The venter of western Mexican specimens is dark reddish brown instead of being fuscous or black as in other color forms. This effect, however, seems to be inherited multifactorially, the F_1 hybrids being intermediate and the F_1 and backcross progeny showing a wide range of variation in ventral coloration which is very difficult to assay.

It is clear from these crosses that the head pattern does not show the degree of dominance of the light patterns which is shown in the pronotal and elytral patterns. This has also been evident in previous crosses of other color forms but in most is difficult to quantify because of the close resemblances of the head patterns. In all the present crosses, the female or male parent from the lightly pigmented western Mexican form showed head pattern 8 in which the pigment does not extend anterior to the arms of the epicranial suture. Only about 8% of the wild specimens from the Rio Presidio show any indication of a darker pattern, and these all have the pigment barely exceeding the arms of the epicranial suture and were rated as 7. In the F_1 of crosses with the darker forms, darker head patterns were common: 95% with AYA (Fig. 15), over 80% with WHR (Fig. 18), and 100%with BIV (Fig. 21). These results are also confirmed by a number of other crosses in which smaller numbers were involved and which are not included in the totals in the figures.

In F_1 crosses and backcrosses of $AYA \ge WAL$, the partial dominance of the lighter head pattern is maintained (Figs. 16-17) as also seems to be the case in the F_1 crosses of $WAL \ge WHR$ (Figs. 18-19). In the crosses of hybrids of $WAL \ge WHR$ with AYA and with backcrosses and crosses of $WAL \ge BIV$, however, scattering occurs (Figs. 20, 22-24) with only partial segregation into two modes (Fig. 24).

In all the crosses the pronotal and elytral patterns show clearer indications of dominance and segregation in the F_1 , backcrosses, and crosses with other strains. Although the numbers are small, segregation is marked in the F_1 and backcrosses of $AYA \ge WAL$ as might be expected from the very different patterns of these two forms. The evidence of segregation is less evident in the crosses of $WAL \ge WHR$ and $WAL \ge BIV$, and $WAL \ge WHR$ crosses some interference may be present which reduces the darker classes.

The $WAL \ge BIV$ hybrids are remarkable in that in backcrosses and crosses with AYA, types of pronotal and elytral patterns appear

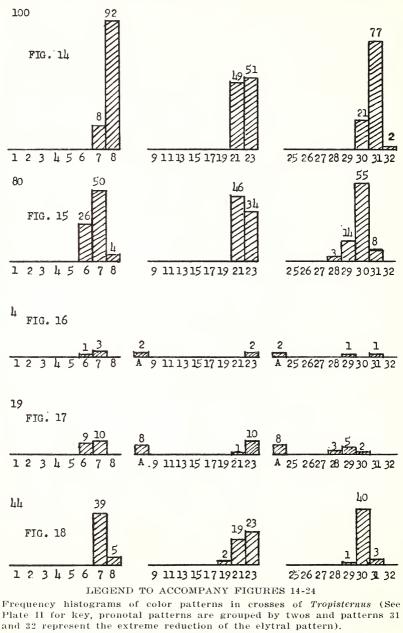
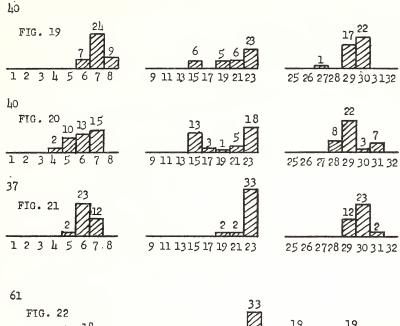


Figure 14. WAL and VUN, wild and reared specimens from Rio Presidio, Sinaloa, Mexico.

Figure 15. Hybrids of AYA x WAL Figure 16. F1 crosses of AYA x WAL Figure 17. Blackcrosses of AYA x WAL Figure 18. Hybrids of WAL x WHR

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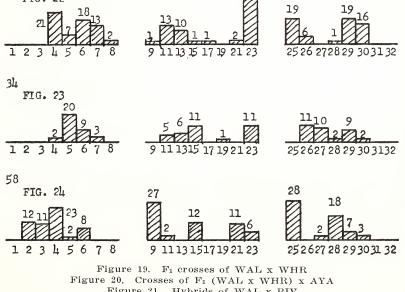


Figure 21. Hybrids of WAL x BIV Figure 22. Crosses of F₁ (WAL x BIV) x AYA (male) Figure 23. Crosses of F₁ (WAL x BIV) x AYA (female) Figure 24. Backcrosses of WAL x BIV which are characteristic of the wild populations of *striolatus*. The suggestion, however, that *striolatus* actually represents a hybrid population between *viridis* and typical *mexicanus* is still unacceptable. The population of *striolatus* is too uniform over too great an area (2). A possible explanation is that *viridis* (*BIV*) carries the pattern genes for the *striolatus* (*WHR*) pattern, and that the extension of the pattern is due to unrelated genes.

The results reported here do not seem to indicate the breakdown of a supergene, but may best be explained on the basis of segregation of modifiers of a major gene or genes.

Summary

A lightly pigmented form of *Tropisternus* (s. str.) from western Mexico was crossed with color forms *striolatus* (LeConte) and *viridis* Young and Spangler and with a melanic form of *collaris* from Colombia. The pronotal and elytral pattern of the light form showed dominance over the darker patterns in all crosses, but the lighter head pattern showed partial dominance. F_1 crosses, backcrosses, and crosses with the South American melanic form showed higher variability and partial segregation into the parental types. The results are interpreted as being most probably due to the segregation of modifying genes which affect the details of the major color patterns.

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