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COLOR-PATTERN IN LEPIDOPTERA

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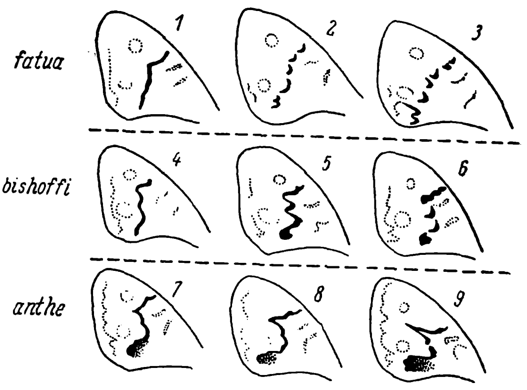
During the last three decades the investigation of the color-pattern of Lepidoptera was progressing considerably both concerning its morphology, ontogeny and cryptic properties. In the present paper a brief summation of the work mainly of the USSR workers is to be given that being mostly restricted to the wing-pattern of Lepidoptera.

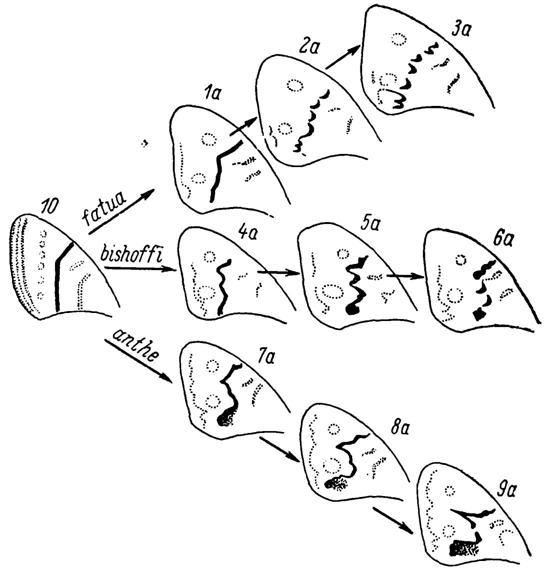
I. MORPHOLOGY

The principal method of the analysis of wing-pattern in Lepidoptera is that of studing the variety of its individual components in the imago to build up morphological series and then to interpret the latter. The method allows to study the almost innumerable forms of all the continents.

Portmann in his book (1932) deals with the evolution of color-pattern. He described e. g. a series of the wing-patterns of Lepidoptera after Henke (1933) which are undoubtedly evolving from one another and says that without some supplementary, e. g., palaeontological, evidence the direction of its evolution cannot be recognized and the process might be equally considered as either a simplification or complication.

But were it so no pattern investigation on its present scale would be possible. The Swiss author is right only in the fact, that without some supplementary data it is really impossible to «read» the direction of evolution in a single morphological series. But the difficulty persists only until dealing with the isolated series and disappears at once on remembering the basic method of comparative anatomy i. e. comparison of closely allied forms. Let us consider e. g. the forms of the first medial stripe (made in black, figs. 1—9) in *Satyrus.* There are two extreme forms of it. In *S. fatua* — a continuous slightly curved one (fig. 1) and one dissolved into a series of unicellalar fragments (fig. 3). In *S. bischoffi* the extreme conditions of the stripe are the continuous and fragmentated ones (figs. 4, 6) but the fragments are located ladder-like (fig. 6). In *S. anthe* we find the continuous condition (fig. 7) and with a long denticle (fig. 9). All the three species exhibit intermediate conditions between the extreme ones (figs. 2, 5, 8). None of the series affords any indication as to the direction of the variability. The evolution from fig. 1 towards fig. 3 is as likely as that in the opposite direction. But a comparison of all the six widely divergent conditions shows that three of them diverge at the utmost (figs. 3, 6, 9) while the remaining three are practically similar (figs. 1, 4, 7). Consequently the latter represent a condition in common to all the three species. As far as the evolution passes from general conditions to specialized ones the above demonstrates which is the direction of the variability in every of the three species (fig. 1a—9a) and consequently it should be concluded that the interrupted, ladder-like and denticle shaped forms of the stripe M^1 are really originating from its primitive shape shown in the diagram (fig. 10). On the basis of this fairly old method a number of wing-pattern have been analysed belonging to many families of the Lepidoptera and thus shown that inspite of the greatest divergencies of patterns studied they all derive from some common source. The results thus obtained are corroborated by the experimental work of German authors on the ontogenesis of wing-pattern. E. g. the Anlagen of different pattern components proved to be different as to the periods of their appearance in the pupa (Koehler and Feldotto, 1935).



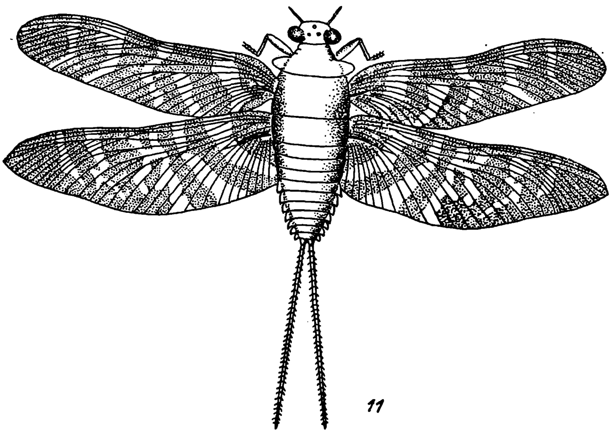


Figs. 1—9. Variability of the first Medial strips (Made in black) in three *Satyrus* species. 1—3 — *S. fatua* Frr., 4—6 — *S. bischoffi* v. *eginus* Stgn., 7—9 — *S. anthe* v. *enervata* Alph.

Figs. 1a—9a. The same *Satyrus* specimens as in figs. 1—9 but placed according to the directions of the variability of the first Medial stripe. 10— primitive form of the same stripe.

The prototypes or schemes of the wing-pattern proposed by different workers (Schwanwitsch, Süffert, Henke) somewhat diverge from one another. But their essence is the same viz. first the wing-pattern consists of several systems which though coordinate into a whole are nevertheless independent from one another and second the phenomenon of secondary symmetry is typical of the structure of some of them. Let us consider the prototypes of wing-pattern as used in the work of the present author.

The wing-pattern of insects in general has not yet undergone any systematic study. But in its most generalized form it seems to consist of broad stripes transverse to the wing. In *Doropteron mirum* (Hemiodonata, Perm) six of them may be recorded on the fore wing and seven on the hind one (fig. 11). It is noteworthy that they seem to originate from a continuous pigmented area broken off into the stripes, the division not being everywhere completed. The number of seven has been indicated by Van Bemmelen (1919) as primitive for the Lepidoptera and the same we met in Lemche's work (1937) with. In the Lepidoptera the maximum of this sort of stripes recorded by myself is three; though the *Micropterygidae* possibly possess a fourth one but the group has not been studied by myself yet. Accordingly the trinominal prototype (fig. 12) valid for the *Tortricidae* and *Hepialidae*



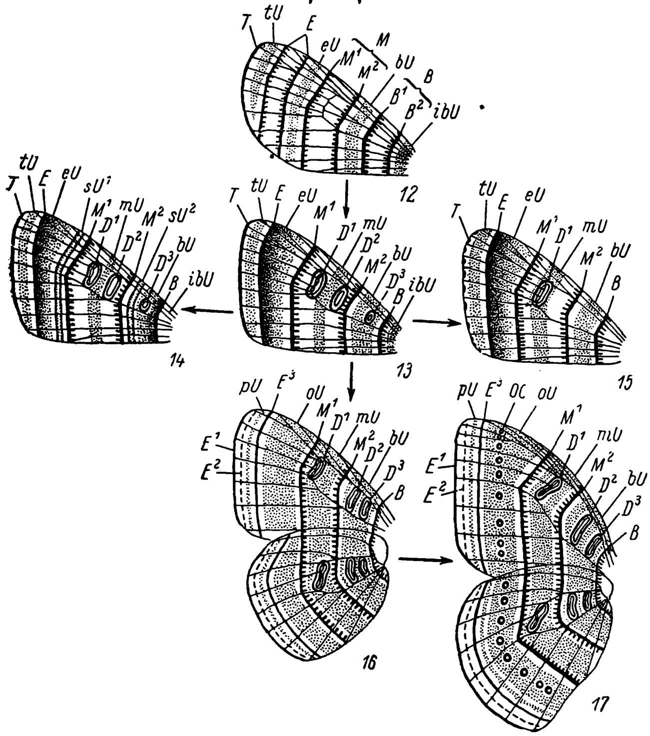


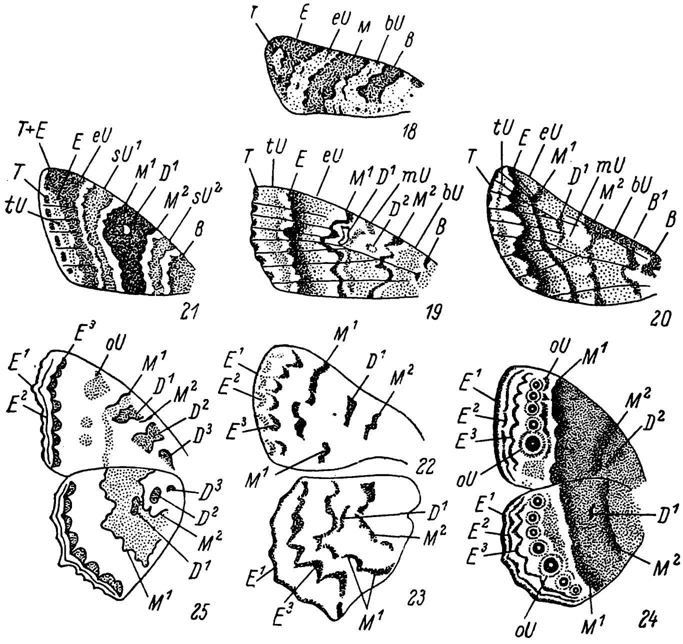
Fig. 11. *Doropteron mirum* Zal. (Hemiodonata, Perm). From Zalessky.

Fig. 12—17. Prototypes of the wing-patterns of Lepidoptera. 12 — trinomial, 13 — first mediodiscal, 14 — second mediodiscal, 15 — simplified mediodiscal, 16 — general rhopalocerous. 17 — nymphaloid.

Lettering. *B* — Basalis, B^1, B^2 — first and second Basalia, D^1, D^2, D^3 — first, second and third Discalia, D^2p — posterior portion of D^2, D^3d — distal portion of D^3 (macula sagittata), *E* — Externa, E^1, E^2, E^3 — first, second and third Externae, *M* — Medial system, *M. s* — its broken off part, M^1, M^2 — first and second Mediae, M^1b — ring budded off from M^1, M^2b — ring budded off from M^2, *OC* — eye-spot, *T* — Terminalis.

bU — basal Umbra, *eU* — external Umbra, *eU6* — portion of *eU* in the 6th cell, *ibU* — infrabasal Umbra, *mU* — medial Umbra, *oU* — ocellar Umbra, *pU* — peripheral Umbra, sU^1, sU^2 — first and second supplementary Umbrae, *tU* — terminal Umbra.

consists of three broad stripes or rather systems — External, Medial and Basal (**E, M, B**). In every of them the margins are darker than the middle, i. e. a subdivision into two symmetrical halves takes place. Between these components a system of scantily pigmented Umbrae is located (**tU, eU, bU, ibU**) while along the termen a narrow stripe passes (**T**). Some intermediary forms not to be described here lead to the first mediodiscal prototype valid for the huge bulk of Heterocera including Pyralids (fig. 13). Here the medial system becomes culminating ($\mathbf{M}^1$ $\mathbf{M}^2$) and one more Umbra



Figs. 18—25. Wing-patterns resembling the prototypes represented in figs. 12—17. 18. *Tortrix chrysantheana* Dup. *Tortricidae* (cf. fig. 12); 19—*Spinterops spectrum* R. *Noctuidae* (cf. fig. 13); 20 — *Thaumatopoea herculeana* Rmbr. *Thaumatopoeidae* (cf. fig. 15); 21 — *Euchera* sp. *Drepanidae* (cf. fig. 14, from Süffert, 1927); 22 — forewing of *Satsuma frivaldskyi* Ld. *Lycaenidae* (cf. fig. 16); 23—Hindwing of *Thecla niphon* new. *Lycaenidae*; 24 — *Mycalaesis* sp. *Satyridae* (cf. fig. 17); 25 — *Vanessa urticae* L. (from Köhler u. Feldotto, 1935).

has developed inside it (**mU**), the basal system has contracted and lost its proximal half while the external system loses its symmetry and consists of a single stripe (**E**) which the external Umbra (**eU**) emanates from as it were. To the enumerated components the system of Discal spots is added consisting of three roundish markings of symmetrical structure ($\mathbf{D}^1$, $\mathbf{D}^2$, $\mathbf{D}^3$). the two distal ones representing well known reniform and circular spots of Noctuids.

In the second mediodiscal prototype a pair of supplementary Umbrae stripes each split along ($\mathbf{sU}^1$, $\mathbf{sU}^2$ in fig. 14) are added to the above, while the Basal system (**B**) consists of a stripe with an Umbra emanating basifugally from it so that the **E, eU** and **bU, B** form now a symmetrical pair.

In the simplified mediodiscal prototype (fig. 15) $\mathbf{D}^2$ and $\mathbf{D}^3$ are wanting owing to their occurring rather seldom while the stripe **T** has, as it is common, dissolved into unicellular fragments. The principal prototype of the Rhopalocera (fig. 16) differs from first mediodiscal one in the three External stripes (**E**^{1}, **E**^{2}, **E**^{2}) being present instead of two (**T**, **E**) and in the **D**^{2} being situated beyond the Medial system (fig. 16) instead of inside of it (fig. 13). The prototype is valid for the *Papilionidae*, *Lycaenidae* and *Hesperidae*. The Nymphaloid one (fig. 17) embracing five families differs in the presence of the eye-spots series (**OC**) in the area of the ocellar Umbra (**o**U) the latter corresponding to **e**U of the Heterocera. In figs. 18—25 some real patterns are given that illustrate the described prototypes. Fig. 18 corresponds to the trinomial prototype, fig. 19 to the first mediodiscal prototype, fig. 21 to the second one, fig. 20 to the simplified one, fig. 22, 23 to the general rhopalocerous prototype and fig. 24, 25 to the Nymphaloid one.

In figs. 26—51 the results are represented of the morphologal analysis of more than forty wing patterns of moths and butterflies. The full analyses of them are either published or under publication elswhere. To abbreviate the representation only the final extreme forms are afforded while all the intermediary ones are omitted. Most of the analyses belong to the present author but several of them are borrowed from Henke (1936), Henke and Kruse (1941) and from Sokolov (1936, 1947) but the diagrams of those patterns are given in the present author's system.

A. Heterocera

1. *Pyralidae. Nymphula nymphaeata* (fig. 27) — the narrow posterior part (Ms) of **M**^{1} **M**^{2} has broken off from the broad anterior one, the lattes being divided into two by the large **D**^{1}. *Crambus hamellus* (fig. 28) — **M**^{2} is sharply bent, so that its fore and hind parts have become almost longis tudinal thus forming a narrow basifugal corner that enters the system **M**^{1} **M**^{2}.

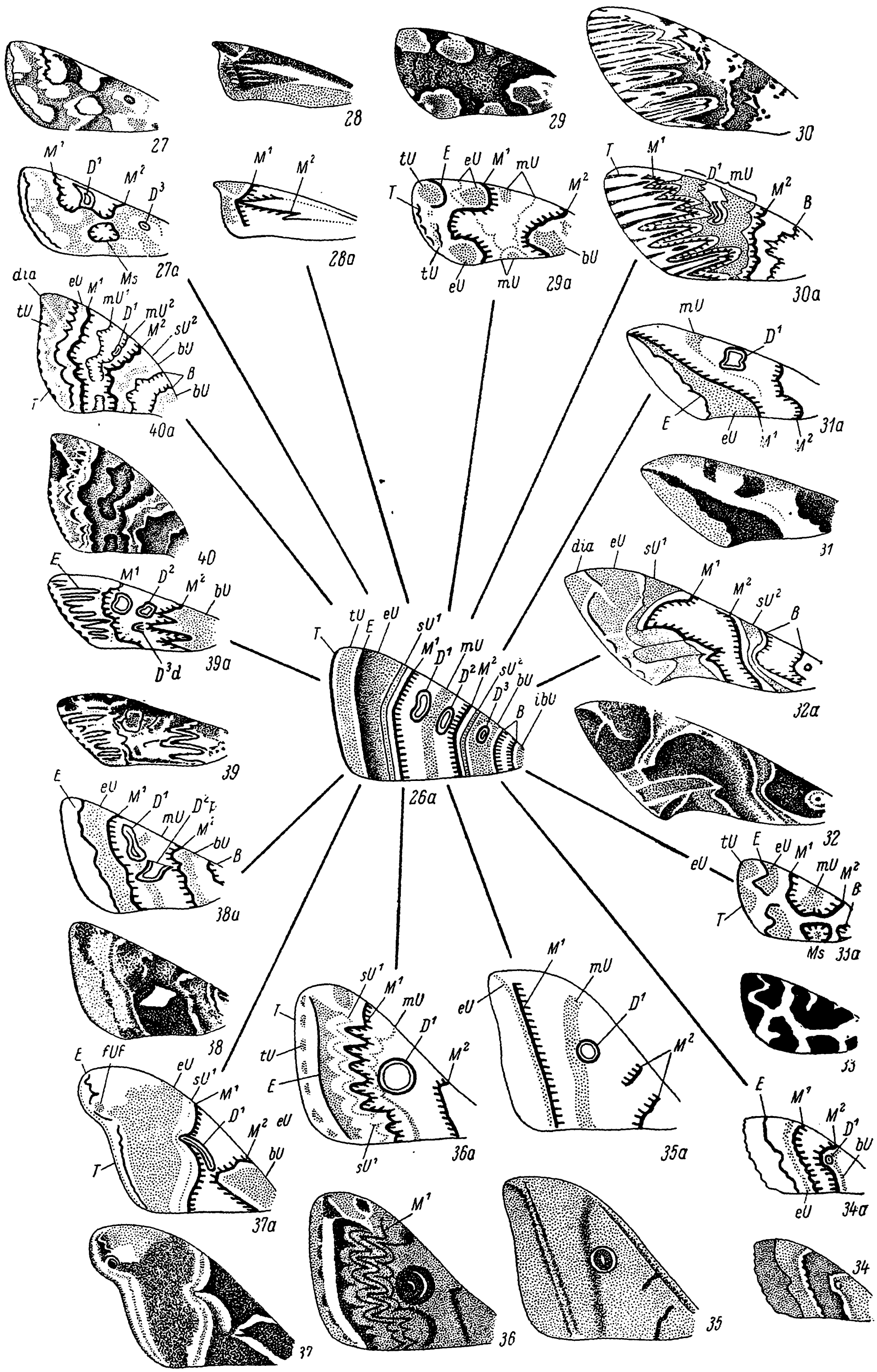
2. *Cymatophoridae. Thyatira batis* (fig. 29) — four large rosewhite markings derive from the Umbrae (**t**U, **e**U, **b**U) and the surrounding interspaces, the boundary of the apical marking being formed by the strips **E** those of the middle and basal ones by **M**^{1} and **M**^{2} resp.

3. *Notodontidae. Dicranura felina* (fig. 30) — **M**^{1} has extended basifugally along the nervures thus forming large sharp denticles. The same is the case of the stripe-like margin of **m**U, the foremost part of the latter component having moreover divided into two halves. The stripe **T** forms a series of long interveinous bars.

4. *Sphingidae. Deilephila euphorbiae* (fig. 31) — **M**^{1} has come to lie along the diagonal (apico-basal) line of the wing and has met with **E** at the apex. The space between the two stripes is filled up by the Umbra **e**U. *Daphnis nerii* (fig. 32) — **M**^{1} produces a beak like basifugal protrusion in the middle cells, while **s**U^1 has largely expanded in the three posterior cells, and **e**U does the same in the anterior ones. **B** and **dia** (apical diagonal) are present.

5. *Arctiidae* (after Sokolov, 1936). Both stripes and Umbrae expand and darken hugely. *Arctia caja* (fig. 33) — the middle parts of **M**^{1}, **m**U

Figs. 26—40. Wing-pattern of 14 species of moths. Figs. 26a—40a. Diagrams of the wing-pattern of the same species. Lettering and graphic representations as in figs. 12—17. 26 — Heterocerous prototype amalgamating characters of the first and second mediodiscal prototypes (13, 14). Figs. 27—28. *Pyralidae*. 27 — *Nymphula nymphaeata* L., 28 — *Crambus hamellus* Thnbg. Fig. 29. *Cymatophoridae*. 29 — *Thyatira batis* L. Fig. 30. 30 — *Dicranura vinula* v. *felina* Btl. Fig. 31—32. *Sphingidae*. 31 — *Deilephila euphorbiae* F., 32 — *Daphnis nerii* L. Fig. 33. *Arctiidae*. (After Sokolov, 1936), 33, — *Arctia caja* L. Fig. 34. *Lasiocampidae*. (After Sokolov, 1947). 34 — *Dendrolimus pini* L. Fig. 35—37. *Saturnidae*. (After Henke, 1936). 35 — *Antheraea* sp., 36 — *Caligula boisduvali* Ersch., 37 — *Philosamia cynthia* Dr. Fig. 38—39. *Noctuidae*. (After Henke u. Kruse, 1941). 38 — *Phytometra aemula* Schiff., 39 — *Cucullia asteris* Schiff. Fig. 40. *Geometridae*. 40 — *Lygris prunata* L.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and M^2 fuse together forming a sort of trident, the latter's posterior part (Ms) has broken off from the rest.

6. *Lasiocampidae* (after Sokolov, 1947). *Dendrolimus pini* (fig. 34) — the spot D^1 has left the area of the $M^1 M^2$ system and comes to lie proximal to M^2.

7. *Saturnidae* (mainly after Henke, 1936). *Antheraea* sp. (fig. 35) — the rectilinear M^1 has approached the terminal border of the wing, the postdiscal portion of M^2 has shifted basipetally and broken off from the rest (pierellisation). *Caligula boisduvali* (fig. 36) — M^1 protrudes into basifugal interveinous denticles and has become sinuous. The same is the case of mU and sU^1, while the denticles of eU are basipetal and enter between these of sU^1. *Philosamia cynthia* (fig. 37) — the M^1M^2 system is constricted in the middle cells with the result that M^1 is pierced by D^1 and the latter partly comes to lie outside the medial system.

8. *Noctuidae* (after Henke u. Kruse, 1941). *Phytometra aemula* (fig. 38) — D^2 is absent but its postdiscal supplement (D^2p) is filled up by metal shining scales. *Cucullia asteris* (fig. 39) — E and M^2 extend into a number of very long loops while in M^1 no modifications are to be noticed. D^3d (macula sagittata) is present.

9. *Geometridae. Lygris prunata* (fig. 40) — mU is split along into two stripe-like halves (mU^1, mU^2), the basal component (B) and apical diagonal (dia) are well developed.

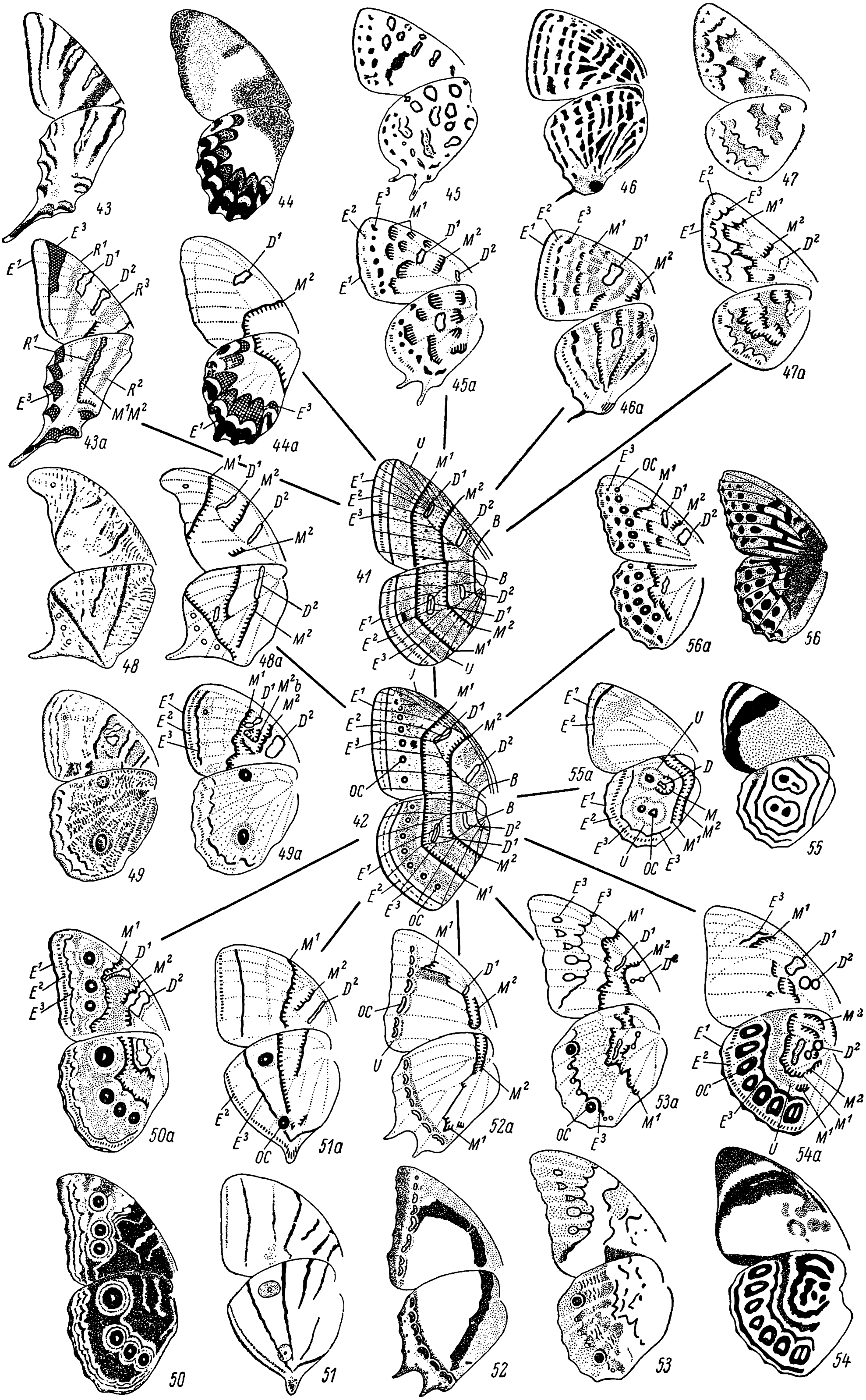
B. Rhopalocera

1 (10). *Papilionidae.* In a part of species the Umbrae transform themselves into stripes which may be longitudinally splitted and filled up by red pigment being accordingly termed Rubrae (R^1 R^2 R^3). The stripe E^1 also tends to subdivision but is filled up by blue.

On the forewing of *Papilio podalirius* (fig. 43) E^3, R^1 and R^3 are present but R^2 is lost (though existing in some subspecies). On the hindwing R^1 has approached to the narrowed system M^1 M^2 and shows orange pigment instead of the red one. The most remarkable modifications are: on the forewing a basipetal dislocation of the posterior parts of R^1 and M^1 and on the hind one the terminal position of E^3 which is due to the atrophy of the terminal zona of the wing together with E^1. The pattern has markedly degenerated on the forewing of *Papilio erechteus* (fig. 44) while on the hind one the widely expanded E^1 and E^3 are predominating which character is typical of a number of Papilios. The interspace between E^1 and E^3 is red.

2 (11). *Lycaenidae* show three tendencies viz. longitudinal subdivision of stripes, their cellular fragmentation and the strialisation of Umbrae. *Cigaritis cilissa* (fig. 45) is devoid of Umbrae, most stripes have dissolved into unicellular fragments and a number of the latter are shaped circular owing to their incomplete division. The fragmentation of components rea-

Fig. 41. General prototype of the wing-pattern of the Rhopalocera. Fig. 42. Prototype of the wing-pattern of the Nymphaloid families. Fig. 43—56. Wing-pattern in 14 species of Rhopalocera. Fig. 43a—56a. Diagrams of the wing-pattern of the same species. Lettering and graphic representation as in figs. 12—17. Fig. 43, 44. *Papilionidae. Papilio podalirius* L.; 44 — *Papilio erechteus* Don. Fig. 45, 46. *Lycaenidae.* 45 — *Cigaritis cilissa* v. *maxima* Stgr.; 46 — *Zephyrus saepe striata* Hew. Fig. 47. *Hesperidae* 47. *Hesperia sidae* Esp. Fig. 48. *Satyridae.* 48 — *Caerois chorinaeus* F. Fig. 49. *Brassolidae.* 49 — *Opoptera acadina* Latr. Fig. 50. *Morphidae.* 50 — *Morpho narcissus* Stgr. Fig. 51. *Amathusiidae.* 51 — *Amathuxidia dilucida* Hb. Figs. 52—56. *Nymphalidae.* 52 — *Charaxes arja* Feld.; 53 — *Prepona eugenes* Bates; 54 — *Agrias lugens* Stgr.; 55 — *Callicore meridionalis* Bates; 56 — *Argynnis paphia* L.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ches a climax in *Zephyrus saepestriata* (fig. 46) and coupled with the strialisation of Umbrae it results in a presence of some 92 markings on the two wings.

2 (12). *Hesperiidae* exhibit a basifugal dislocation of the forewing anterior part of M^1 and «albinisation» of the M^1 M^2 system on the hind wing. The latter consists of the interspace between M^1 and M^2 growing either white or at least lighter than the adjacent umbral areas. *Hesperia sidae* (fig. 47) moreover shows a basipetal shifting of the anterior hindwing portions of E^3, M^1 and M^2.

Satyridae, *Brassolidae*, *Morphidae*, *Amathusiidae* and *Nymphalidae* are pooled together on the basis of the nymphaloid scheme of pattern (fig. 42).

4 (13). *Satyridae.* In both wings of *Caerois chorinaeus* (fig. 48) M^1 has dislocated basifugally, while the postdiscal portiones of M^2 have shifted basipetally and having coalesced with D^2 form complex stripes (pierellisation) (Schwanwitsch, 1925, 1928). Externae are rudimentary which possibly depends upon the atrophy of the zone of wing margin.

5 (14). *Brassolidae. Opoptera acadina* (fig. 49) — a large ring-shaped portion (M^2**b**) has budded off from M^2 basifugally and come to lie between M^1 and M^2. A basipetal dislocation of eye-spots and numerous strioles on the hindwing, are noteworthy.

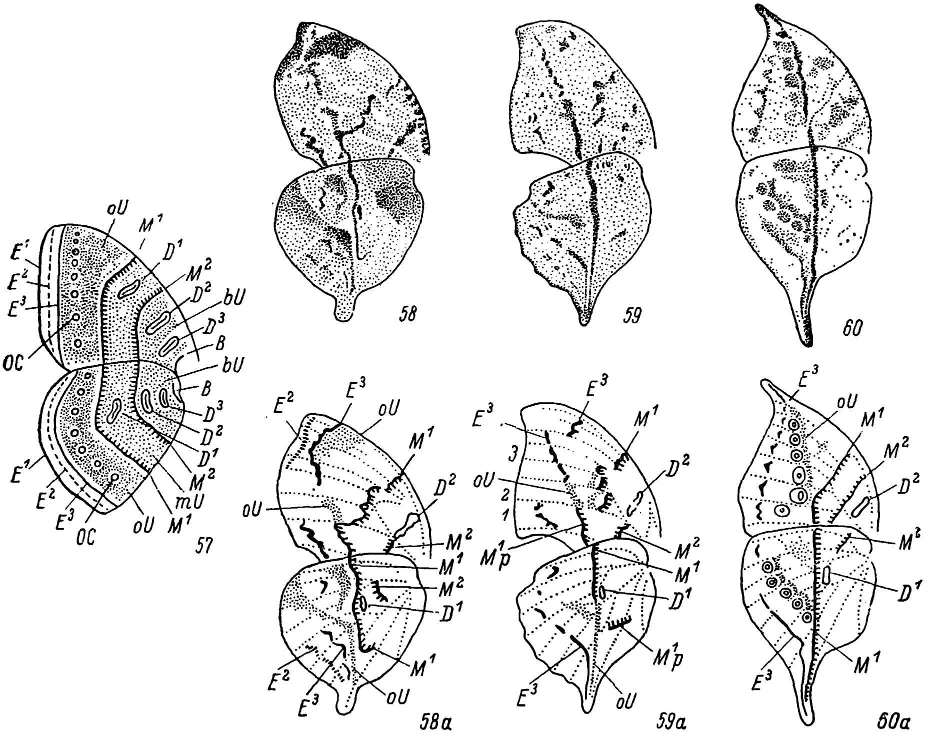
6 (15). *Morphidae* are rather primitive and show all the main components. In *Morpho narcissus* (fig. 50) the Umbrae are very wide especially on the hindwing, the enlarged eye-spots press, as it were, on the components near by without contacts however.

7 (16). *Amathusiidae. Amathuxidia dilucida* (fig. 51) has feeble Umbrae but most of the stripes are retained and shaped rectilinear. A remarkable phenomenon is that the posterior eye-spot is «superposed» on the stripe E^3 and the latter seems to be translucent through the former.

8 (17). *Nymphalidae.* In *Charaxes arja* (fig. 52) the interspace between M^1 and **o**U, has greatly expanded and pushed far away the system M^1M^2 basipetally and **o**U with the eye-spots basifugally. The eye-spots have grown reniform, the zone of the Externae is not analysed yet. On the fore wing of *Prepona eugenes* (fig. 53) series of rings has budded off from E^3 while the stripe itself is dislocated basipetally. On the hind wing E^3 is similary dislocated but the eye-spots holding their positions have passed through the stripe and come to lie distally from it i. e. the two components have exchanged their places. On the hindwing of *Agrias lugens* (fig. 54) the latter process has advanced further. But moreover several complex components are present on the hindwing, i. e. the posterior portion of M^1 occupies the place of disappeared **o**U portion, while in the former's place a correspondingly dislocated portion of M^2 is situated. A partial exchange of places in D^2 and M^2 is noteworthly and two curvations of the anterior portions of M^2 to M^1 are noteworthly. The forewing pattern is markedly atrophied. A similar degenerescence is observed on the forewing of *Callicore meridionalis* (fig. 55). On the hindwing the middle of the M^1M^2 system has shifted basipetally like in *Charaxes arja.* But a portion of M^1 remains stationary, and has budded off from its maternal stripe. It encircles D^1 and is fused with the umbral circle that surrounds the anterior eye-spot. The complex component thus evolved resembles the umbral circles of the two posterior eye-spots.

In *Argynnis paphia* upperside (fig. 56) E^2 and E^3 have dissolved into unicellular fragments which resemble the depupillated eye-spots present. The E^3 fragments are internervural while those of E^2 lie on the nervures. The general fragmentation is coupled with an abundant representation of the prototypical components.

The described examples which a number of others could be added to prove that the most divergent wing-patterns of Lepidoptera really originate from the same ground source. If the latter is represented by six prototypes that is due to the fact mainly of technical grounds as e. g. it is hardly possible to locate **D**^{2} in two different places in the same scheme: viz. beyond the Medial system (Rhopalocera) and inside of it (Heterocera), also it is impossible to figure the system **E** both in the symmetrical and unilateral conditions and so on. But nevertheless it is evident that all the six prototypes represent different sides of the same ground plan of the wing patterns.



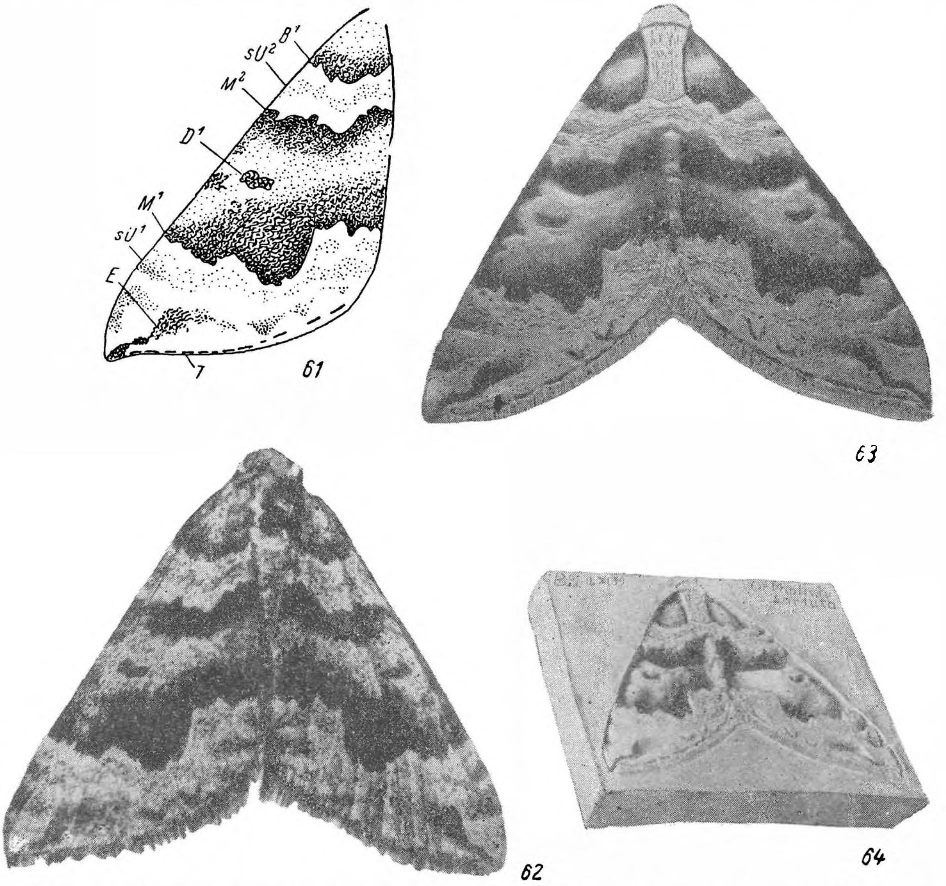
Figs. 57—60. Morphology of dead leaf wing-patterns in the *Nymphalidae*. 57 — Nymphaloid prototype; 58 — *Siderone marthesis* v. *nemesis* Ill.; 59 — *Zaretes isidora* v. *strigosa* Stgr.; 60 — *Kallima inachis* Boisd.

Figs. 57a—60a. Diagrams of the wing-patterns of the same species. Lettering and graphic representations as in figs. 12—17.

The modification of the prototypes are very different but they are specific for every group, though a given modification may occur in two distant patterns. The main modification however is undoubtedly the dislocation either of the total component or oftener of some part of the latter affecting the general form of a given component in a number of ways. Also the disappearance of components, their coalescence, division, formation of complex stripes are met with being however mostly derived from dislocation. Melanisation stands apart, the appearance of new components is uncommon. In general the modifications themselves are comparatively simple but the occurrence of several of them in a single wing-pattern may afford to the latter a considerable complexity the latter being made out only by the method of morphological analysis.

II. CRYPTISM

The biological value of cryptism has been proved by a number of workers. Among the others the investigation by Schwarz (1950) is noteworthy carried on in the deserts of Central Asia and elsewhere in the USSR. In a definite locality the percentage is estimated of insect species both in the field and in the stomaches of insect-feeding birds as e. g. *Coracias garrulus*, during its hunt. The percentage of cryptic insects in the stomach proved to be lower than in Nature and sometimes nil as in the case of e. g. *Acrida turrita*, while the non cryptic forms as e. g. *Blaps* are oftener met with in the stomach of *Coracias* than in the field. Consequently the cryptoma, i. e. the total of cryptic characters viz. color, body form and pose, really protects insects from predators.



Figs. 61—64. Stereomorphism in the Geometrid *Ortholitha sartata* Alph. 61 — wing-pattern of *O. sartata*; 62 — photo of a specimen; 63 — monochrome sculptural model of the same specimen; 64 — the same from the side.

With regard to the morphology of cryptoms it should be pointed out, that sometimes the more modified are the components of the wing-pattern, the more exactly some biotop model is imitated. E. g. in the dead leaf imitator *Siderone* the stripe M^1 is uninterrunted though shows marked dislocations (fig. 51). In *Zaretes* M^1 divided into several portions foreshadoved in *Siderone*, and having united with isolated portions of E^3 and **oU** results in much more perfect imitation of the central nervure of a dead leaf (fig. 59). In *Kallima* studied by Eimer (1896) and Süffert (1927) the same model is reproduced otherwise (fig. 60).

Stereomorphism consists of the fact that the flat wings of Lepidoptera exhibit reproductions of some imaginary elevations and depressions that may be percepted by means of some stereoscopic devices, as e.g. Pigeon's stereoscope and the illusion of the relief thus obtained may be reproduced in monochrome three dimensional models. So e. g. the medial system of stripes in a quiscent *Ortholitha sartata* (figs. 61—64) reproduces

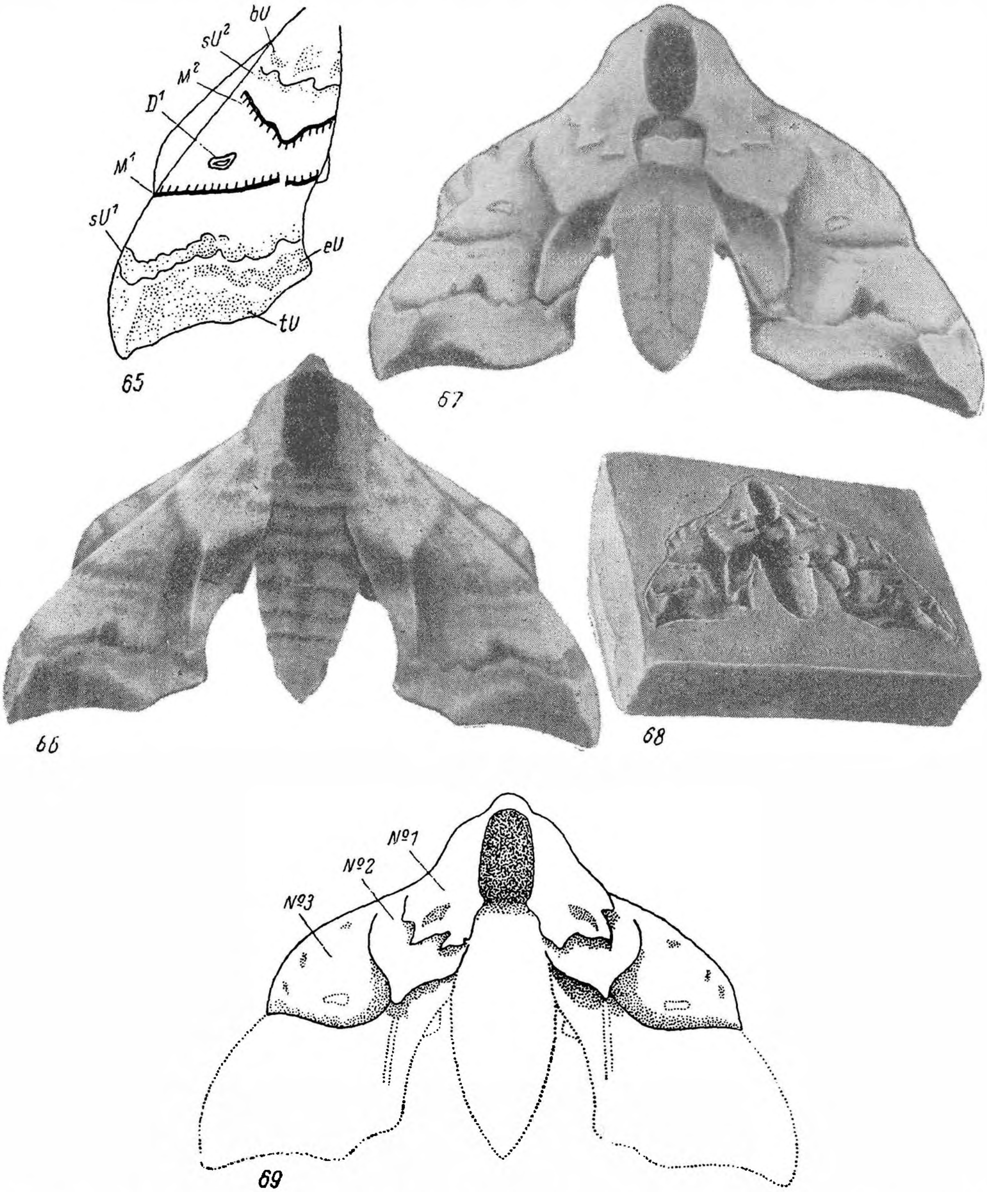
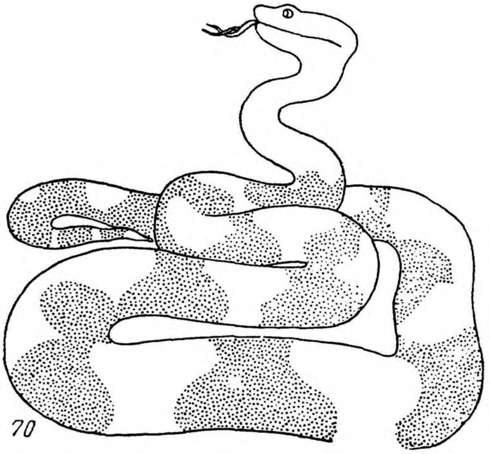


Fig. 65—69. Stereomorphism in the Sphingid *Smerinthus ocellata* L. 65 — diagram of the wing-pattern; 66 — photo of a specimen; 67 — monochrome sculptural model of the same specimen; 68 — the same from the side; 69 — diagram of three dead leaves in the wing-pattern (see text p. 58).

a broad groove with a somewhat elevated middle of its bottom and overhanging borders (fig. 63). In a more complicated stereomorphic cryptom of *Smerinthus ocellata* (figs. 65—69) the reproductions of three overlapping leaves may be discerned (fig. 69) one with broken border (N 1), another with attenuated tip (N 2) and a third (N 3) placed partly on the hind wing border protruded from under the fore one. A number of other examples of stereomorphism has been described by the author in the Lepidoptera (1938, 1943). A reproduction of some imaginary bodies on the flat wing much enhances the concealment of the latter especially if placed among the real relief of the biotop. Thus owing to stereomorphism flat surfaces are visually relieved and three dimensional while owing to the principle of counter shading (Thayer 1909) curved surfaces seem flat. Stereomorphism is observed in many other animals including Vertebrata. The first example of it though without ascribing cryptic value to it has been described by Darwin (1871) in the plumage of the pheasant *Argusianus argus*. The images described by him of the balls in pits may be reproduced in sculptural model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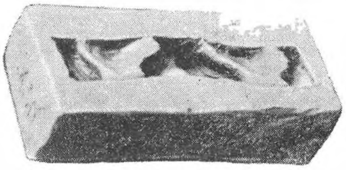
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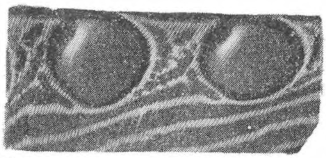
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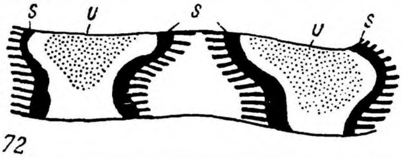

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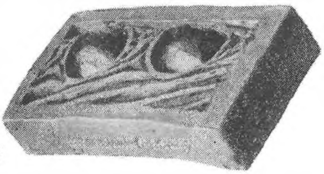
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Fig. 70—73. Stereomorphism in snakes. 70 — *Ancistrodon contortrix* L. From Brehm's Tierleben. Only two light marking of the series are represented; 71 — monochrome sculptural model of these spots; 72 — diagram of the model — light markings (U) resemble the Umbrae of the Lepidoptera, dark ones (S) correspond to the symmetrical systems like the Medial system of Lepidoptera; 73 — the same model from the side.

Fig. 74—76. Stereomorphism in the pheasant *Argusianus argus* L. 74 — photo of a feather portion; 75 — sculptural model of it; 75 — the same from the side.

(figs. 74—78) where the balls themselves are made shining to reproduce the reflections from walls seen in them. The dark spots of the snake *Ancistrodon contortrix* (figs. 70—73) are also stereomorphic and again represent depressions with elevated middle of the bottom and overhanging margins (fig. 71) a general construction of the cryptic spots. The spots of the *Argusianus* spots differ from the general standard only in their circular shape and strong elevation of the bottom middle.

Green reflex principle (Schwanwitsch, 1945) is based on the importance of illumination for the cryptic effect. If e. g. a *Colias* is sitting with closed wings among the grass the green reflexes from the plants transform the yellow coloration of the underside of wings into a green that does not differ at all from the general hue of vegetation and thus a strong cryptic effect arises. A more specialized example affords *Phytometra* (*Plusia*) *chrysitis* (fig. 77). The yellow metallic areas of its wings serve perfect booking-glass that reflects exactly the green of the foliage if the moth is sitting deep enough among the plants. The indicated areas thus become practically invisible while the remaining yellowish brown parts of the body show an irregular shape of a scorched dead leaf utterly dissimilar to any insect. Undoubtedly the phenomenon is widespread among the animals and its cryptic significance is evident.

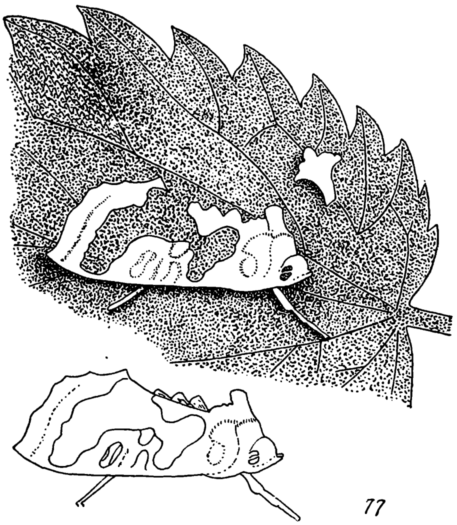

Fig. 77. Green reflex in *Plusia chrysitis* L. Metal shining areas of the wing reflected the green color of the nettle and are practically invisible thus the shape of the moth being utterly distorted. Below the total shape of the moth. From Schwanwitsch, 1945, 1949.

SUMMARY

1. The studies of the color pattern of Lepidoptera, mainly carried on in the USSR with remarks on Vertebrata are briefly reviewed.

2. A principal method of studying wing-pattern in the imago is that of building up morphological series of individual pattern components. To find out the direction of the evolution of a given component a comparison of several series of it is necessary. No single series may reveal the evolutionary direction.

3. Three broad transverse strips, or systems of symmetrical structure — Externa, Media and Basalis — are the main components of the trinomial prototype valid for the primitive Lepidoptera. In the mediodiscal prototype of the Heterocera the medial system becomes dominant, the External one loses its symmetrical structure and a system of three Discal spots is added to the rest. The general rhopalocerous prototype as compared to the preceding one has three peripheral stripes instead of two and shows the extra medial position of one of the Discal spots instead of the intra medial one. The Nymphaloid prototype differs from the preceding one in having a series of eye-spots. Two more prototypes of a secondary importance are added to the medio-discal one.

4. Some 28 wing-patterns of the Heterocera and Rhopalocera chosen from a much greater number are shown to be reduced to the above prototypes.

5. Biological value of cryptism is shown by a number of authors and by the Soviet author Schwarz (1950) among them.

6. The maximum resemblance to biotop models and maximum modifications in the morphology of pattern are often concomitant.

7. Stereomorphism i. e. the presence on the wing of two dimensional images of three dimensional biotop models makes the flat wing surface visually relieved and thus enhances the cryptic effect. Stereomorphic color-patterns are not restricted to the Lepidoptera but occur in other animals including Vertebrata (*Argusianus*, *Ancistrodon*) too.

8. By the green reflex principle the fact is meant that some surfaces of the body especially the shining ones may reflect the green of the vegetation and thus become visually as green as the latter, the cryptic effect being thus heightened.

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РЕЗЮМЕ

Морфологический анализ рисунка взрослых чешуекрылых ведется следующим образом. Строятся ряды индивидуальной изменчивости данного компонента рисунка у нескольких близких видов. Каждый отдельный ряд не указывает направления изменчивости, но при сравнении

нескольких рядов одни их концы оказываются различными, а другие сходными. Сходство указывает на общность основы всех рядов, и таким образом выясняется направление изменчивости для каждого ряда. Этот метод позволил построить прототипы рисунка для Rhopalocera и Heterocera и связать с прототипами ряд рисунков из обеих групп. В настоящем сообщении предлагается шесть прототипов для различных групп чешуекрылых. Объединение всех прототипов в одну схему технически невозможно, но все они имеют общую основу, которая слагается из не более чем трех широких поперечных полос, имеющих симметричную структуру, из умбр, лежащих в промежутках между ними, и из трех небольших пятен так называемой дискальной системы, также имеющих симметричную структуру. Часть Rhopalocera имеет добавочную систему глазчатых пятен. Приводятся, как пример, рисунки 46 видов Lepidoptera, анализированных на основе указанных прототипов, что составляет небольшую часть всех опубликованных анализов. Изменчивость рисунка состоит главным образом в многообразных смещениях его компонентов и их частей по крылу. Результаты данного метода исследования подтверждаются и изучением онтогенеза рисунка.

Эффективность криптизма подтверждается многими полевыми исследованиями, в том числе и советских авторов (Шварц). Усиление морфологических изменений рисунка ведет к повышению сходства с растительными моделями.

Криптический эффект усиливается посредством стереоморфизма: путем применения специальных стереоскопических методов показано, что на плоских крыльях многих бабочек находятся изображения некоторого рельефа, который можно воспроизвести на одноцветных скульптурных моделях. Явление показано также для рептилий и птиц (*Ancistrodon*, *Argusianus*).

Криптический эффект у чешуекрылых усиливается благодаря «зеленому рефлексу»: отдельные незеленые участки крыльев становятся визуально зелеными, отражая зеленые лучи в глубине травы.

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