THE *KARANASA* BUTTERFLIES — A CRITICAL REVIEW

by E. G. MUNROE

The sumptuous work of A. Avinoff and W. R. Sweadner entitled "The *Karanasa* Butterflies, a Study in Evolution" *(Annals Carnegie Museum,* vol. 32, art. 1: 250 pp., 17 pls.; 1951) will stand as a worthy monument to its authors. The way that tragedy struck twice during the preparation of the work, preventing each of the authors from seeing the finished product of his labours, is narrated in a brief memorial note at the front of the volume. It is our good fortune that Dr. Sweadner was able to see and correct the final proofs of the book, which he did with rare devotion on what proved to be his death-bed.

Those who had the privilege of knowing Dr. Avinoff and Dr. Sweadner will see their personalities reflected in the content and composition of their monograph. Dr. Avinoff's zeal and imagination, his ability to surmount apparently insuperable difficulties, his love of the romantic aspects of lepidopterology, and his life-long enthusiasm for the fauna of central Asia are all shown in the very choice of the project, which occupied his attention for many years. These qualities, together with a fine historical sense, a close acquaintance with the foremost lepidopterists of Russia and western Europe, an intimate personal knowledge of the remote and desolate region which forms the habitat of *Karanasa,* a remarkable command of the English language, a passion for detail in taxonomy, and an outstanding technical ability in all that pertains to the production of both text and illustrations of fine books, made Dr. Avinoff's contribution to the study a dominating one. To these already great resources were added Dr. Sweadner's broad background in biology, his painstaking methodology, and his carefully considered and highly original ideas on species-structure and speciation.

The result is a treatise which represents more than merely a detailed study of a restricted group of butterflies from the Pamir region. On the one hand it is a volume that is reminiscent of the traditions of a more opulent era: one which might well have appeared as a Romanoff "Mémoire" or an Oberthür "Étude"; on the other hand it is a valuable and provocative contribution to the study of evolution and species relationships.

As a monograph and a guide to the identification of the butterflies of the group *Karanasa,* the book leaves little to be desired. The populations are for the most part clearly differentiated, and are described and figured in the most exhaustive detail. Some of the named populations are known only from very short series, but in every case of this kind there is reason at least to suspect that a distinguishable entity exists. The authors are, moreover, careful to specify that their naming of these forms is tentative, the aim being to avoid confusion of poorly known but possibly distinct forms, such as has so often caused trouble in the past.

The higher classification adopted, and the associated evolutionary interpretation, are, however, likely to prove more controversial. Since this book is certain, because of its importance for students of speciation and zoogeography, to attract attention far beyond the comparatively limited circle of those interested in the butterfly fauna of central Asia, I feel that a brief discussion of these more general aspects will not be out of place here.

The authors, with considerable justification, adopt as the basic units of their classification the smallest recognizable populations. These populations, each considered to be separated from all others by geographic, altitudinal, or reproductive barriers, are named, and are treated as subspecies. The higher classification is achieved by grouping the unit subspecies in four ranks of successively more inclusive categories. In some cases the second, in other cases the third, of these ranks is taken as being equivalent to the species, but the authors make it clear that they regard the species as a purely nomenclatorial concept, which has, in this group at least, no real counterpart in nature.

Before this general conclusion can be examined, we must consider the subspecies grouping in greater detail. The highest category of Avinoff and Sweadner's scheme, the "fifth category" or "division", provides a convenient basis for such a consideration. Avinoff and Sweadner recognize five divisions. Each is morphologically characterized; each occupies a definite part of the Pamir mountain-system; the range of each definitely overlaps that of one or more other divisions, and in such zones of overlap the members of the sympatric divisions are always clearly distinct. Within the divisions, on the other hand, the relationships of the subspecies are complex and often obscure. For this reason, an individual discussion of each division is desirable.

At this point I must mention certain deficiencies of presentation that make critical analysis of the taxonomic arrangement difficult. One of these is the inadequacy of the maps provided to elucidate the ranges cited in the text. The most complete map is that given in Fig. 5, opposite page 47, in which the type localities of all the subspecies are indicated by number. The numbers refer to the sequence of the check list on pages 194 to 196. The check list numbers are also given, but often out of sequence, in the main descriptive text, pages 47 to 148. Mr. N. Shoumatoff has pointed out to me that the discrepancies in sequence mainly result from the attempt to give the oldest name in any one group first in the text arrangement, whereas a purely systematic sequence is given in the check list. There are also, however, four errors in the numbering of the forms in the main text, as follows:

Number Given in Text	*Should Read*
69	68
70	69
67	70
68	67

Although the map is complete as to type localities, it omits a large proportion of the other localities cited in the text. These are frequently obscure; good maps of the region are not easy to obtain, and in consequence many of the localities must, even for the careful reader, remain meaningless. Maps purporting to give the ranges of the various subspecies are given in the section "Categories of Higher Order", pages 167 to 188, but the ranges are in fact indicated only by crudely drawn outlines, which are of little value for detailed analysis, and are in some cases misleading, *e.g.,* in the probably erroneous range attributed to the form *tancrei* in Fig. 16 and, by implication, in Fig. 13. In none of the maps is there any attempt to indicate relief, although the configuration of the mountain systems must have been well known to the authors and is of the greatest importance in the taxonomic situation.

The remaining weaknesses lie principally in the presentation of quantitative aspects of the data on which the study is based. The number of specimens examined is specified for only about two-thirds of the named forms; there is often no clear differentiation in the enumeration of specimens available for study at the time of writing and those examined earlier at the British Museum or those that were in Dr. Avinoff's collection prior to the Russian Revolution. Considerable weight is given to variation in genitalic and androconial characters among the various populations, but there is no indication of how many genitalic preparations were made, or of how the samples of androconia were taken or from how many specimens. There is no mention of the size of samples or of the statistical procedures used in deriving the average dimensions of the androconia and in assigning the androconia of the various populations to the six arbitrary categories that are used to characterize them. Beyond the statement that "the scales from any individual specimen vary very little and those from any individual population vary only slightly more" (p. 42), there is no effort to assess the extent of variation in androconial measurements within populations or to demonstrate the significance of such variation among populations. A similar vagueness is found in the descriptions of subspecies. Although this is partly offset by the numerous and excellent illustrations, it makes it hard in most cases to assess the variability of whole population-samples or to judge the reality of the discontinuities in variation between certain supposedly distinct populations. It is true that subjective assessments of variation and of discontinuity in variation are customary in taxonomic descriptions of Lepidoptera, but one would certainly have expected to see stronger and more explicit supporting data for such subtle and perhaps disputable distinctions as are proposed in, for instance, the *josephi-wilkinsi-intermedia* complex.

It is very probable that these faults, which are largely of omission rather than of commission, would to a considerable extent have been corrected by the authors had they been able to complete their work at greater leisure and under happier circumstances. I mention them simply to show how room is given for some of the skepticism that I shall express in following paragraphs, room that might have been greatly lessened by a more explicit presentation.

Turning now to the detailed consideration of the subspecies aggregations, we may consider first the *pamira,* or "specialized unbranded", division. Here we have a comparatively simple pattern of six subspecies, arranged in a north-south cline-like series, with a single short offshoot to the east in the central Pamir region. The authors treat this division as a simple polytypic species. No other interpretation seems possible.

Next in order of complexity is the *bolorica,* or "primitive branded", division. Here again we have a simple series of replacement-races, but the division occupies a larger territory and forms a more complex geographic and taxonomic pattern than does the *pamira* division. Avinoff and Sweadner recognize three species: *voigti* from the western Hindu Kush, *bolorica* from the central and eastern Hindu Kush, and *decolorata* extending from southwest Pamir along the northern slope of the Amu Darya basin. There appears to be a fairly definite taxonomic break between the *decolorata* and the *bolorica* groups. The forms of the bolorica group are smaller, duller, and sharper-winged than those of the *decolorata* group. They have more slender

androconia and stouter processes of the gnathos, and their valves lack terminal tubercles. These distinctions do not, however, appear to be absolute. The southern populations of the *decolorata* group show modifications in the direction of the slender androconium, the thorn-like gnathos, and the aborted terminal tubercle. Moreover, specimens referred on the basis of external appearance to *bolorica,* but apparently not structurally investigated, have been taken at Alitchur, in south Pamir, north of the Amu Darya Valley, which appears to form the main frontier between the *decolorata*-like and the *bolorica*-like forms. It seems at least possible that the genetic leakage which is apparently taking place here is across a geographical and not a biological barrier.

The southerly *voigti* complex (known from one female of the "subspecies" *voigti* and one pair of the "subspecies" *nigrocellata*) is *decolorata*-like in facies, and has, according to the description, a well-developed terminal tubercle; on the other hand the androconia are like those of *bolorica* and the gnathos may be taken as an extreme development of the *bolorica* type.

My inclination would be to include all the forms of the *bolorica* division in a single polytypic species, an arrangement not ruled out by Avinoff and Sweadner, although they did not adopt it. All the named forms are fully allopatric, and there is no conclusive, or even very strong presumptive, evidence of important sterility barriers within the division. That *bolorica* in this sense is specifically distinct from the southern members of the *josephi* division appears to be shown by the reported co-existence of the very distinct forms *grumi* and *darwasica* at Visharvi Pass.

A more difficult problem is presented by the members of the *huebneri,* or "specialized branded", division. This division has an arcuate range to the south of the main crests of the Hindu Kush and Karakoram ranges. On the basis of maculation, the subspecies can be divided into two principal groups: one characterized by a dark ground and bright, contrasting pattern, the other by a paler ground and pallid, ill-defined light pattern. The first group occupies the whole length of the Hindu Kush, and reappears in a narrow territory extending from the Deosai Plains along the southwest slopes of the Western Himalaya as far as northern Kangra in the Punjab. An isolated population of similar type occurs at Baltoro Mt. in the Karakoram. The second group extends from Astor and the northeast slopes of the Western Himalaya northeastward through the Zanskar and Ladak ranges to the Karakoram; the members of this group become progressively darker from east to west, so that the westernmost populations do not differ radically from the easternmost populations of the first group, which inhabit the opposite slopes of the Western Himalaya. An apparent exception results from the incursion of a tongue of the range of the pale northeastern subspecies *balti* between the ranges of the darker *astorica* and *expressa;* this is mentioned in the text, but is not shown in the distribution map on page 185. Thus a British Museum series referred to the pale *balti* is labelled as coming from the type locality - Deosai Plains - of the dark *modesta* of the western group. Avinoff and Sweadner conclude that the western and eastern groups of subspecies are specifically distinct. They state: "In any one locality (the members of the dark western group) are fairly easily separated from their lighter neighbours". Examination of the localities listed shows, however, that the only ones in which specimens of both groups have been taken are the Deosai

Plains and Rohtang Pass, at the north and south ends, respectively, of the crest of the Western Himalaya. The situation at Rohtang Pass is poorly understood, owing to the possible mislabelling of some of the specimens. No direct evidence is given that the two forms from the Deosai Plains actually fly together; I do not have enough geographical information on the locality to judge whether or not the two series may have come from separate colonies, from eastern or western slopes, or from different altitudes. There is indeed, characteristically, no indication of how large the two Deosai Plain series are, or of how sharp and how constant are the differences between them. To provide supporting evidence for the differences between western and eastern groups the authors state, without elaboration, that the variation of the pooled populations is distributed bimodally. This condition may well be the consequence of physical separation by the barrier of the Western Himalaya, and not the result of physiological separation by a partial or complete reproductive isolation.

At the southern end of the Western Himalaya, in the Rohtang Pass, an additional form lacking androconia has been taken. This is supposed to co-exist with dark and with light androconia-bearing forms. The situation is complicated by the possible mislabelling of some of the material. It may be, as Avinoff and Sweadner suppose, that the form without androconia *(rohtanga)* is a good species, but I think it more likely that it is an extreme variant, perhaps representing a semi-isolated population on the west side of the pass. I think it very unlikely that the two androconia-bearing forms are specifically distinct. When it is remembered that the whole of the material from Rohtang Pass consists of fourteen specimens, of which two are considered to be definitely and four to be possibly mislabelled, the difficulty of assessing the true situation becomes obvious.

A second form with androconia occurs in the general vicinity of Astor, to the north of the Punjab Himalaya. This form differs also in wing shape and in four apparently independent characters of maculation from the sympatric androconia-bearing forms. Although it is not the only tenable hypothesis, I think it at least fairly likely that this form *(cadesia)* is a distinct species. The remaining forms of the *huebneri* division I should be inclined to consider as subspecies or variants of a single species, although certain doubtful points remain to be cleared up before this view can be accepted with absolute confidence.

A somewhat similar but perhaps less difficult problem is presented by the *regeli,* or "fuscous-and-ivory", division. This has the most northerly range of the divisions of the genus, extending from the Alai Mts. north to the Alexander Mts. and eastward into the Tian Shan and Boro Khoro ranges. Avinoff and Sweadner would recognize three species in this division. They separate these on characters which appear to me, on the basis of the figures and illustrations given, to be completely intangible. There are three supposed areas of overlap of the "species". In the general region of the Alexander Mts. four subspecies are shown on the distributional maps (pp. 178-181) as occurring. Of these, *tancrei* and *latifasciata* are stated in the text to be of doubtful provenance; *kirgizorum* is not only of doubtful origin but is referred in the text to another division. This leaves a single subspecies, *kasakstana,* as an undisputed inhabitant of the region. Farther to the south, *occidentalis,* listed as a subspecies of *latifasciata,* occurs at Naryn, to the west of the

range of typical *latifasciata* and in the range of typical *abramovi. Occidentalis,* however, is based on a single specimen, a dwarfed and suffused individual that looks to my eye much more different from *latifasciata* than that form does from *abramovi.* It is my opinion that *occidentalis* probably represents an individual variant or a high-altitude from of *abramovi,* and that it has no especially close relationship to *latifasciata.* The third supposed zone of overlap is in the southern part of the range of the division, in the neighborhood of the Tchatyr-Kul. Here four forms are listed as occurring, of which one is referred to the "species" *abramovi* and three to *regula.* An examination of the figures given, however, particularly Figs. 15 to 19 and Fig. 28 of Plate 10, suggests strongly that only a single variable population exists in this district. The report by Erschoff, cited on p. 109, of two forms (presumably *regeli comradti* and *abramovi abramovi)* flying together without intermediates is so vague that it is probably fair to minimize its significance.

Apart from these extremely doubtful instances of overlapping, the various members of the fuscous-and-ivory division form a very neat group of replacement-races. If the illustrations of the various subspecies are examined in geographical sequence with this interpretation in mind, they seem to form a smoothly graded series, and I accordingly believe that they would best be treated as components of a single species.

The last major group recognized by Avinoff and Sweadner is the *josephi,* or "russet unbranded", division. This ranges from the Alexander Mts. south to the northern side of the Amu Darya Valley in the west and to the northern Karakoram in the east. It is thus at least partly sympatric with each of the four other divisions. From the *pamira* and *huebneri* divisions it is distinguished by clear morphological characters. From the *regeli* division it has no major structural differences, but differs very widely in maculation in localities where the two fly together, as is well shown in Plate 8. The figures on this plate, by the way, represent a taxonomic and not a geographical "ring": the superficially most similar forms of the two divisions live farthest apart, instead of in adjacent territories as might be inferred from the arrangement; in order to show the geographic relationship, the figures in the left-hand column should proceed upward and not downward from Fig. 1. Finally, from the *bolorica* division the *josephi* division differs in that its members lack androconia. It is true that the androconia are weak in the subspecies *roborowskyi* of the *bolorica* division and that the genitalic differences between the contiguous populations of the two divisions are by no means striking. However, as I have mentioned, the two divisions appear to co-exist, without mingling, at Visharvi Pass.

Avinoff and Sweadner consider that the *josephi* division is composed of "an irreducible minimum of three" species. I regret that after careful examination of the figures and descriptions I find it very hard to accept this conclusion. It seems to me most unlikely that in the second column of Plate 8, representing the so-called "ring" already mentioned, Figs. 8, 10, and 12 are of one species, Figs. 9, 11, and 13 are of a second, and Fig. 14 is of a third. Avinoff and Sweadner adopt their interpretation chiefly because of the occurrence of three supposedly distinct forms in certain regions of the Alai and Transalai ranges, notably at Taldyk Pass, although it is freely admitted that the same forms intergrade at other places. Space does not allow me to review the various populations in detail, but an account of the general dis-

tribution pattern seems desirable. In the south, from the northern Karakoram to the Transalai, is found a series of small, dull, pallid forms in the high-altitude passes. On the lower ground to the west, and less markedly at moderate altitudes in the east, these forms intergrade with or are replaced by larger, more brilliant, fulvous-marked forms. These, together with certain individuals of the second type from the Transalai and Alai, are grouped by Avinoff and Sweadner as the "species" *leechi.* A second group of fulvous forms in the northwestern Pamir and the Transalai and Alai is grouped with a number of subspecies from the ranges north of the Syr Darya under the name *josephi.* I am unable to appreciate the differences between the *josephi* and the *leechi* forms in the western Alai and Transalai, and I believe that they in fact constitute a single interbreeding population or geographical group of populations. In the eastern Alai and Transalai the paler forms *wilkinsi* and *robusta* are found. I think that these are pale subspecies replacing the darker western complex and that the supposed zone of overlap at Taldyk Pass is simply a blend zone of the eastern and western races. Avinoff and Sweadner, however, also include in the "species" *wilkinsi* three subspecies from mountain ranges well to the north across the very wide basin of the Syr Daria. In my opinion these races have been artificially torn out of the series of northern races that Avinoff and Sweadner refer to *josephi,* of which they seem to me to form an integral part. To recapitulate, I believe that the members of the *josephi* division can best be treated as subspecies of a single species: a series of small alpine subspecies *(e.g., leechi)* in the south, intergrading on the west to a second series of bright, large subspecies *(e.g., darvasica, intermedia),* which extends northward through the western Alai and across the Syr Daria to the northwest Tian Shan, giving off a lateral series of pale populations *(wilkinsi, robusta)* in the eastern Alai and Transalai.

In short, I think there are excellent reasons for reducing Avinoff and Sweadner's "minimum" number of twenty species given in the check list to seven and possibly to five. When this is done, what happens? The baffling problems of evident gene-interchange across species lines disappear; they existed only because the lines did not demarcate species in the biological sense. On the other hand, there is little if any evidence of gene-interchange between divisions, and in general the divisions appear to me to represent the natural species of this group.

Avinoff and Sweadner would undoubtedly have argued that this is a superficial view, that there are discontinuities and overlaps within the divisions too great to be accommodated within the limits of a single species. I believe, however, that many of the apparent discontinuities are the result of faulty sampling - obviously hardly to be avoided when the nature and limited quantity of the material are considered; other discontinuities, believed by Avinoff and Sweadner to be determined by reproductive behaviour, are in my opinion probably the result of simple geographic, environmental, or genetic factors. The struggle to characterize the elusive and inconstant differences of *"wilkinsi", "leechi", "intermedia",* and *"josephi"* seem to me to be typical of the sort of difficulty one often encounters in the initial stages of investigation of a species problem, when one is grappling with what eventually prove to be imaginary, or at least intraspecific, differences.

I have dwelt at length on the apparent weaknesses of the taxonomic treatment because, although this treatment is fundamental to those aspects of

the paper which will interest the general student, it will not be readily accessible to criticism by the non-lepidopterist. The recognition of these weaknesses should not, however, be permitted to obscure appreciation of the many admirable features of the book, of which I have tried to give some indication in the first part of this review. Taking the over-all view, I do not hesitate to say that this is a most valuable work, magnificently produced, and representing an intensive, conscientious, and in most respects very accurate study of a group of great intrinsic interest. It is a book that I am glad to have on my shelf, one written by distinguished entomologists whom I am proud to have numbered among my friends.

Acknowledgement

I wish to thank Mr. Nicholas Shoumatoff, New York, for carefully reading a preliminary manuscript of this review, and for making a number of constructive suggestions. I do not wish to imply, however, that Mr. Shoumatoff necessarily subscribes to the statements or criticisms made herein; for these I take full responsibility.

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PERSONALIA

The death of Dr. ROBERT LOELIGER was recently reported here (*Lepid. News* 6: p. 78). The continuation of the Circulaire of the *Centre d'Observation pour les Migrations de Papillons,* which he founded and maintained, has been undertaken by two members of the Groupe. These new editors are EUGÉNE PLEISCH, Regensberstr. 30, Zurich 50, and HANS SIDLER, Goldregenweg 21, Zurich 50, Switzerland, Dr. LOELIGER'S final *Circulaire* was No. 38. No. 39/40, by Mm. PLEISCH and SIDLER, is dated August 1952. In it are reported 1952 migrations through North Africa and Europe of *Vanesssa cardui, Celerio livornica,* and other Lepidoptera. An interesting observation by ANTHONY VALLETTA, of Malta, concerns two *Danaus chrysippus* which had apparently arrived from Africa with the *V. cardui; D. chrysippus* had not been seen on Malta since 1943.

CYRIL F. DOS PASSOS has been appointed a Research Associate in the Section of Insects and Spiders of the Carnegie Museum, in Pittsburgh, Pennsylvania. For many years Mr. DOS PASSOS has been a Research Associate of the American Museum of Natural History, in New York. The Carnegie Museum has a long tradition of developing notable collections of Lepidoptera (see Sweadner, *Lepid. News* 2: p. 80; 1948). HARRY K. CLENCH is now the lepidopterist on the Museum staff.

The editorship of *The Entomologist,* the well-known British monthly periodical, has passed from Mr. N. D. RILEY to Mr. D. LESTON. Mr. RILEY, Keeper of the Department of Entomology in the British Museum of Natural History, is responsible for the largest and both taxonomically and geographically most complete research collections of insects in the world. At present he is President of the Royal Entomological Society of London. In addition to these and other positions of responsibility, as well as his notable researches on the Lepidoptera, Mr. RILEY has been for many years a most effective Editor of *The Entomologist.* He remains as an assistant editor.