

REVIEWS

WARREN'S ARGYNNID CLASSIFICATION (NYMPHALIDÆ)

by L. P. GREY

A second section of WARREN'S revision of Argynninae came out in 1955, devoted to Asiatic species, extending his study which appeared in 1944. He salvages what there was of value in the earlier haphazard work of REUSS and incorporates therewith results of his own investigations.

In dealing with "*Argynnis*" and "*Brenthis*" and arguing for splitting of these familiar (one might almost say hallowed) genera, WARREN provokes controversy. His viewpoint is that the genitalic heterogeneity indicates great evolutionary fragmentation, that the similarities in wing pattern are a wholly false gloss giving deceptive appearance of uniformity to what essentially is a phylogenetic radiation of specialized and only remotely interrelated groups.

Through structural definitions made possible by his and REUSS'S studies of the male sexual apparatus WARREN attempts to state categorically a natural phylogeny. Usually, he cites several characters in distinguishing categories, but a couple of examples will suffice to illustrate the tenor of the work, as follows: The Argynninae key from other butterflies by the character of unique membranous area dorsad on the tegumen. The two tribes key by structure of the aedeagus: basally open in argynnids, basally closed in bolorians. Similarly, the genera recognized are keyed by references to structural characters peculiar to the included species.

The supra-generic recognitions are of natural groups customarily recognized as such. The special virtue of WARREN'S systematizing is in the manner of definition. Formerly, these questions of interrelationship were judged mostly by the wingspots, whereas now there is reference to anatomical invariabilities. In earlier revisions one can see how various authors shuffled species around when guessing what relationships might be, so WARREN'S structural definitions bring order where there was a very dark subjectivity. These structural data are handy things to know when correspondents send in spotted butterflies from far corners of the earth.

U / Hereafter, the main concern becomes with the hypotheses of relationship as inferred from the one set of characters, those of male genitalia. There is a secondary issue, of whether WARREN'S categorical usages are the proper ones, but this ties to value judgments of other zoological practices and is especially dependent on what is allowed in other lepidopterological classification. MONROE (1949) has ideas on this subject which may be sounder than WARREN'S because more in line with general classificatory needs. It must be observed, however, that MUNROE discriminates clearly between the two things involved, between the problems of natural relationships and species affinities and the manner of tagging them by categorical devices. Only the former questions, those of morphology and phylogeny, will be considered herein, with no attempt to say what constitutes a "genus."

The generic divisions made by WARREN are the ones most often criticized, and I must ask leave to discuss them with no preliminary explanations, proceeding from the base points as laid down by him. It is out of the question to abstract his text, since it would require about as many words as he uses originally, with loss of richness and originality of meaning, while the text is anyhow only the formal shadow of what best appears in the superb photomicrographs. It is these latter illustrations of the characters of structures which comprise the pith of his work, to be judged only at the source, so that interested students must possess themselves of these references.

The male genitalic variation in *Argynninæ* is for the most part so well described, once and for all, by WARREN, that it would be profitless to rehash those data. There is, however, a huge body of morphological evidence which WARREN makes no attempt to grasp, in the female anatomy, which at one stroke permits a doubling of comparisons and gives some check on the associations as deduced from male genitalia. Having recently surveyed the world species, using both sexes for slide material, I think I see numerous facts cogent to a just criticism of WARREN's phylogenetic assumptions, more to the point than the common notion that "*Argynnis*" should be exempt from analysis, being ordained to amalgamate the spotted butterflies of the world.

Although homologies of parts and phylogenetic value of variations in female genitalia is an obscure field, there are certain differentiations observable in *Argynninæ* which appear to warrant a few conclusions. Chiefly, the fact that the female anatomy is more of a common type in these butterflies, so that congeneric species are rarely separable by this means although the accompanying males often have easily discerned characters, would argue that the more subdued female differences are a more reliable guide to phylogeny when judging supra-specific radiation.

Particularly, these data become a court of appeal when original and radical ideas of relationship are advanced, as in WARREN's latest paper. He asserts therein that the species of *Argyronome* Hübner are to be transferred to the tribe of bolorians, a veritable bombshell of a pronouncement and one which no doubt startled others as greatly as it did me.

This is consistent with what he now accepts as the most important differentiation within *Argynninæ*, the one of ædeagal structure. But the ædeagus of *Argyronome*, even if basally closed, is of a piece with everything else involving those species in being weird. By the wings, these butterflies appear to go with the argynnids; they are very unlike bolorians. But WARREN's thesis all along has been that the wing superficialities are no proper guide to phylogeny. The female anatomy cannot be regarded so lightly, however, so examination of the facts is in order.

All species commonly accepted as bolorians (the bifid-uncus series, the "*Brenthis*" auct.), with which WARREN would incorporate *Argyronome*, have stubby ovipositor lobes flaring from a broad base, while argynnids have longer and more filamentary apophyses. This one contrast is sufficient to distinguish the tribes, although it is fuzzed a bit by specific variations in length and shape. If more were needed to discriminate between the two groups the differences in the vaginal folds would show the distinct lines of evolution.

Now, I am uncertain if this area between the copulatory notch and the sperm sac (bursa copulatrix) is best termed the "ductus bursæ," the "antrum," or more vaguely if more certainly correctly the "invagination," and it does not matter because students will know from this where to look. In the argynnids this part of the genitalic apparatus is elaborately wrinkled, often sclerotized, there is some sort of a pattern to the wrinkling, usually radiating from a central circularity and in each of WARREN'S "genera" there is a characteristic facies of these "corrugations," but the differences are within such limits that the "genera" could be presumed interrelated. In the bolorians, by way of contrast, this invagination is quite unremarkable, the foldings less ornate and less easily perceived because of the delicacy of the tissues, relieved only by some slightly sclerotized "collar" midway in the tract. Most of the bolorians have a short round bursa copulatrix; the argynnid bursæ are long ovate.

If these differences are any guide to phylogeny it is not reassuring to find that *Argyronome* has an elaborately sclerotized invagination and long ovate bursa. The latter character is a variable one, to be sure; the admittedly bolorian *pales* (Denis & Schiffermüller) series has the bursa more ovate than round, for example. The apophyses are somewhat shorter in *Argyronome* than is normal in the argynnid series, but even if at sea for lack of definitives I would assume that the *Argyronome* species were argynnids rather than bolorians if I saw them as unlabeled genitalic preparations of some unknown derivation, on the general facies. I fail to see that these insects have characters to permit their belonging in Boloriidi, aside from the closed ædeagus.

WARREN insists that the character of ædeagus outweighs all else, which I think raises a most intriguing question and one which is the outstanding curiosity in WARREN'S work to date. Does this structure of the ædeagus root so far back in the gulfs of time that it becomes a touchstone when judging what is ancient and what is more recently acquired divergencies of structure? I have discovered some facts which seem pertinent to this question, suggesting to me that they are precisely the wedge needed to tighten up WARREN'S theories.

This hinges, I think, on the South American Andean series. Regarding these, what little has been written has been inconsequential to a world phylogeny, or has been misleading or false. I have done my share to confuse things and I can only presume that WARREN must have followed an outline drawing made by me when he erroneously relegated this series to *Issoria* Hübner, a drawing which I now find is inaccurate in details as well as miserably contrived in all particulars.

On the face of it, it was ridiculous that this Andean *Yramea* Reuss group could be issorians. If there is nothing else to urge of the phylogenetic adequacy of genitalic data there is the large consistency seen when comparing against geographic distribution, the harmony with what one might expect from past dispersal opportunities, from ancient land bridges, large glacial movements, and the like. What, after all, is phylogeny, if not a community of descent predicated on dispersals? There are issorian argynnids in equatorial Africa and in the foothills of the Himalaya, a gap in distribution made reasonable by similar mammalian dispersals since butterflies ought to be able

to go where elephants have broken the trail. Likewise, the North African argynnids are hardly modified from European forms, as would be expected. Every comparison of group distributions which occurs to me makes good sense, except this one of finding European butterflies in the Andes.

It is time it was known that *Yramea* is not an argynnid genus. In three species recently dissected I find no gnathic development worthy of the name, so they certainly are not issorians. The uncus is singly tipped, but the ædeagus is basally closed, very lightly in the species I drew which may be how I came to overlook it in a single slide, but clearly so in several recent slides.

But the fact which I consider the paramount one to reinforce WARREN'S ideas is that the *Yramea* females integrate with Boloriidi, having stubby apophyses and simple, delicate invagination. In this far isolated group, then, despite many novel structural adaptations, enough persists of common anatomical facies to insure correct tribal placement. And here, it should be highly significant that the ædeagus, conforming to WARREN'S hypothesis, proves to be basally closed.

I think this represents a personal triumph for WARREN. I could not have been happy with his treatment of *Argyronome*, in the face of the incongruities of the female genitalia, but after stumbling on these data of *Yramea* I conclude that his bold venture of incorporating a weirdly anomalous series into the hitherto closely knit bolorian group was a pure stroke of genius, needing only a survey of the Andean forms to extend the precedent and to clothe it in the respectability of world-wide application. Although there is some comfort to those who deplore WARREN'S splitting, because *Argyronome* in some respects bridges his major categorical line, it now seems probable that his key character, which does not fail, is of special phylogenetic value since it persists, as it turns out, in still another offshoot group widely judged to be an ancient divergence.

Being wise after the fact, everybody will now see that when *Yramea* and *Argyronome* enter Boloriidi there will have to be some revamping to accommodate that category to these new conceptions. This spells the end for genera now recognized under *Boloria* Moore; these must sink a notch.

There will remain the problem of the validity of the subdivisions of the *Boloria* series, even as subgenera. It is one thing to criticize, but it is another thing to do the work and to seek for better solutions. Having wrestled with these problems I can better sympathize with WARREN'S avoidance of them. He says that data are insufficient to permit complete diagnosis. I would have said that we have more data than we know what to do with. After the neat splitting of the argynnid series it seemed reasonable to hope that the bolorians might be equally amenable once we knew the world species. The present score is not very impressive. There is *eunomia* (Esper), a species purporting to be a genus, only relatively distinct by male genitalia, and by female genitalia one of an unremarkable series. The female differences suffice to separate most of the species likewise separable by distinctive male armature, but they follow a common plan and thus do not suggest to me any special need for more than the one category. In the genus *Clossiana* Reuss, so-called, there are various species which I think have

equal claim with *eunomia* to special recognition if one were to be consistent in splitting; it may as well be recognized that *Clossiana*, as now constituted, is a catch-all of altogether dubious merit. Although the difference in shape and sclerotization of the ædeagal lobes is a practical help when sorting out the species, WARREN plays this down, and it seems probable that neither these nor any of the other features so far emphasized are of defensible categorical value. It would seem that the uncertainties are a good argument for lumping all species in the one genus until some better way can be found to describe the relationships. I should add that I recognize that the *pales* group is a special divergence, on all counts as aberrant as WARREN claims, but regardless of this the bifid uncus group must close ranks if it is to rub elbows as a category with *Yramea* and *Argyronome*.

WARREN'S arrangement of the argynnid series leaves less chance for differences in opinions; evidence from the female structures would suggest about the same grouping. If the basis for criticism is to be in his synthesis of relationships, only a few minor quibbles would appear possible.

One of these is with his grouping of *paphia* (Linnæus) with *anadyomene* Felder & Felder. By female genitalia *anadyomene* is so distinct that I have been waiting with amusement wondering when the splitters would get around to founding a new genus to accommodate it. The species *paphia* is notable for the highly developed vermicula, which is a most elaborately contrived appendage of the invagination. There is a comparable although smaller and different shaped apparatus in *sagana* (Doubleday). The vermicula has been mentioned as a peculiarity of several species but I have seen it in these two only. I would restrict the term to this sort of extensible appendage as exemplified in *paphia*; it is something quite different from the ordinary "corrugations" of the antrum. One would think that this development indicated something of phylogeny, and if there is to be any equating of these distinctive species it would be *sagana* which I would hold as being nearest related to *paphia*.

WARREN'S assertions of affinities between *Mesoacidalia* Reuss and *Speyeria* Scudder are upheld by similarities of the females, although there is a sharp break. It may be that some future reviewer will see fit to lump these as subgenera within one genus, sinking present subgenera to sections. Whatever formalities may prevail, specialists need not waste energy battling over what angels are to be balanced on what pin-heads. It seems a pity not to work as much of the phylogeny into the systematics as can be discerned and agreed upon, but it is the structural resemblances and differences and what they may indicate of relationships and lines of descent, which general workers as well as specialists will find of interest, regardless of what categorical devices are used in the exposition.

In this review, I have tried to bring out what may be some flaws in WARREN'S organization of the morphological data of Argynninæ. It is a duty to record in strong terms that the bulk of his findings are exactly as one might deduce from independent comparisons of anatomical peculiarities of the females. Aside from the few points mentioned, critics will have to produce some new or better data before decrying the phylogenetic merits of

this classification. WARREN makes admirable synthesis of the male anatomical variation, which is made more certain when it is perceived that the female characters almost invariably support his references.

There will continue to be criticism of his categorical usages, as is quite proper so long as substance is not injured through solicitude for the shadows. "Genera" are but feeble things, rooted in stony ground of tradition and opinion where no amount of harrowing can grow final definitions. The real advances in systematic knowledge come when the interrelationships among species are made known, and here WARREN cites many facts of undoubted truth, of so high a fascination that if there has been any defiance of traditional systematics we can only hope for more of the same.

References Cited

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- ... , 1955. A review of the classification of the subfamily Argynninae. Part 2. Definitions of the Asiatic genera. *Ibid.* 107: 381-392, pls. 1-4, figs. 1-39.

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DIE SCHMETTERLINGE MITTELEUROPAS. By Walter Forster & Theodor A. Wohlfahrt. [In German.] [Sixth instalment, 1955], vol. 2, [8] + 97-126 + [2] pp., text figs. 34-41, colored pls. 21-28. Publisher: Franckh'sche Verlagshandlung, W. Keller & Co., Stuttgart, Germany. Price DM. 10 each instalment.

The previous five instalments of this excellent work — a valuable contribution to lepidopterology and addition to one's library — were reviewed in the *Lepid. News* (vol. 6: pp. 79-80, 1952; vol. 7: p. 26, 1953; vol. 8: pp. 170-171, 1954, respectively).

The sixth instalment of vol. 2 concludes the Lycænidae completing *Lycæides* and continuing with the following genera: *Plebejus*, *Aricia*, *Eumedonia*, *Agriades*, *Albulina*, *Cyaniris*, *Vacciniina*, *Polyommatus*, *Lysandra*, *Agrodiætus* and *Meleageria*. Then is taken up the Hesperioidea, among which are *Erynnis*, *Carcharodus*, *Reverdinus*, *Lavatheria*, *Pyrgus*, *Spialia*, *Heteropterus*, *Carterocephalus*, *Adopæa*, *Thymelicus*, *Ochlodes* and *Hesperia*. In this instalment there are also the title page, preface, table of contents and an index of the generic and specific names used in the butterfly parts. The plates, realistically illustrated in color, conclude the Nymphalidae, and embrace the Libytheidae, Riodinidae, Lycænidae and Hesperioidea.

This completes the butterfly numbers of *Die Schmetterlinge Mitteleuropas*, which is a "must" for those interested in the Palearctic butterflies of Central Europe.

To sum up, volume 1, "Biology of butterflies," consists of xii + 202 pages and 147 illustrations, which may be purchased for DM. 23 linen bound, and volume 2, "Butterflies," consists of viii + 126 pages, 41 text illustrations, 28 plates of 780 colored figures and 29 pages of explanation thereto, which latter volume costs DM. 53 linen bound.

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