

THE HIGHER SYSTEMATICS OF THE BUTTERFLIES

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This paper is a summary of a more extensive work on the morphology, phylogeny and higher classification of the butterflies which is now in press in the *University of Kansas Science Bulletin*.

Despite the great popular interest in butterflies, they have been the subject of relatively little modern systematic work above the level of the generic revision. The interrelationships of the major groups have been poorly understood, and some workers (*e.g.* Clark, 1948) have given family rank to such obviously non-equivalent entities as the papilionids and the argynnids. It is apparent that a mere rearranging of the butterflies on the basis of well-studied characters such as the wing venation or structure of the labial palpi, or the introduction of a new classification based on one or two previously unstudied characters, would be of little significance. Therefore an attempt has been made to reconstruct the phylogeny of the group and arrive at a reasonable classification by utilizing as much published information as possible in conjunction with a comparative study of the multiple characters of the entire integumental morphology.

SYSTEMATIC PRINCIPLES EMPLOYED

Complete objectivity in arriving at classifications and phyletic relationships is at present a utopian concept, although advances are being made in this direction (see Michener & Sokal, 1957). Some major sources of subjective error in taxonomic work are (1) preconception (to some degree unavoidable when a worker is dealing with a group with which he has been long familiar); (2) unjustified character weighting (especially a tendency to give more weight to characters studied personally); (3) group favoritism (the tendency to consider one's "pet" taxonomic group as higher in the hierarchy of classification than equivalent groups); and (4) frankly subjective decisions ("I feel that the X-idæ are worthy of family rank" etc.). Every attempt has been made to avoid these errors in the present work, but doubtless numbers 1 and 2 have not been completely eliminated. It is hoped that 3 and 4, abundantly represented in the literature, have been excluded.

There are those (*e.g.* Warren, 1947) who still claim that higher categories should be based on the distribution of one or two "diagnostic" characters. The repeated failure of systems based on too few characters to stand the test of time is a matter of record, and all modern systematic work is based on the study of as many characters as possible. WARREN'S classification of the butterflies, with its unjustified emphasis on the condition of the prothoracic legs, places the nymphaloid Libytheidæ with the riodinids and separates the lycænids from the riodinids, including them with the Pieridæ and Papilionidæ. This is clearly an unnatural arrangement.

The question of the nomenclatorial status of the various taxa segregated has received considerable attention. Some previous classifications of butterflies, as exemplified by that of CLARK (1948), have presented entomologists

with a mass of poorly defined families, subfamilies, tribes and subtribes in the superfamily Papilionoidea. Fortunately this extreme splitting has been largely ignored. In the present work it has been found that the Papilionoidea divide primarily into five groups. To align the classification of the butterflies with that of other superfamilies of insects, these five groups have been called families (Papilionidæ, Pieridæ, Nymphalidæ, Libytheidæ, Lycænidæ). In their morphology, as in their biology, the butterflies make up an extremely homogeneous superfamily (as compared, for instance, with such groups as the Scaraboidea, Chalcidoidea, Sphecoidea, Apoidea, Fulgoroidea, Tipuloidea, Muscoidea, etc.). It seems evident that the recognition of the primary divisions of the Papilionoidea with superfamilial designations such as "family group" would not be in keeping with accepted entomological practice.

As far as possible the morphological distinctness of the various taxa has been kept uniform within the next highest taxon. Thus, in order to have all the families in the superfamily more or less equivalent, the long standing "families" into which the nymphalids have been split must be considered to be subfamilies, since their retention as families would necessitate the raising to family rank of all the tribes of the Papilionidæ, a move not yet advocated by even the most extreme splitters.

MATERIAL AND METHODS

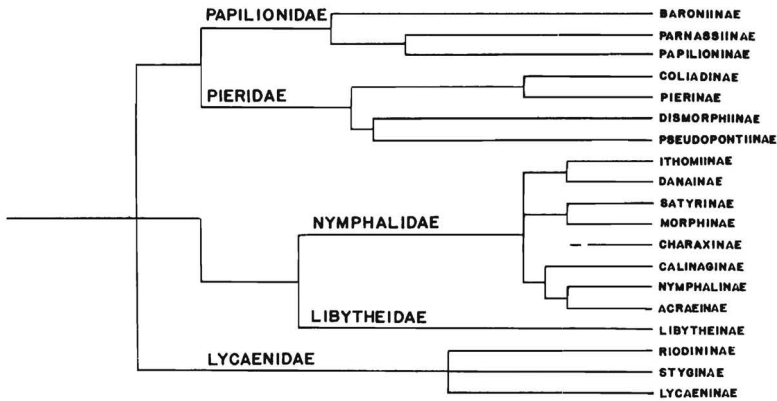
The present study is based on the dissection of some 300 species of butterflies representing more than 240 genera. In addition, representatives of 24 families of moths and skippers were also studied as an aid in determining what were the primitive and specialized states of the characters studied in the butterflies. With the exception of the auxiliary sclerites and the female genitalia all major areas of the integumental anatomy were studied comparatively in specimens which had been boiled in caustic and cleaned of scales and viscera. The above mentioned systems were neglected because a preliminary survey indicated that the value of the data obtained would not be commensurate with the time required for their detailed study.

RESULTS

As would be expected, significant characters were found in all areas of the body, including the internal structures of the head and thorax. Examples of characters (terminology after Ehrlich, 1958a) useful in the higher classification are the shape of the head, the form of the tentorium, the condition of the cervical sclerites, the form of the profurca, the condition of the patagia, the size of the meso-anepisternum, the shape of the lamella of the mesodiscrimen, the form of the third phragma, the general shape of the thorax, the condition of the spiracular bars at the base of the abdomen, and the form of the pretarsus, as well as the more usual characters of the wing venation, labial palps, prothoracic legs and male genitalia. Characters of the larvæ and pupæ have been taken from the literature where available.

More than forty characters have been employed in the family diagnoses. Doubtless many more characters could be found in the integumental anatomy, and the fertile fields of the visceral anatomy and the morphology of the early stages are almost untapped.

The major conclusions of the work are summarized in the accompanying diagram of relationships. The vertical scale is an estimate of what might be called evolutionary distance, being evolutionary rate multiplied by time. It is, of course, impossible to distinguish these two quantities on the basis of neozoological evidence.



Unfortunately there is no room to present the data supporting these conclusions here (the paper being summarized is about 75 pages in length and is illustrated by 64 figures). Some other conclusions are, in brief:

(1) The monster genus *Papilio* (s.l.) is polyphyletic. There is a greater morphological gap between *Graphium marcellus* and *Papilio glaucus* than there is between an *Erebia* and a *Morpho*.

(2) There is little evidence to support many of FORD'S (1944) conclusions on the phylogeny of the Papilionidæ. *Zerynthia* and allies have been included as the tribe Zerynthiini of the subfamily Parnassiinæ. FORD places the Parnassiinæ and Zerynthiinæ at opposite sides of his diagram of relationships. Even accepting without question all of the assumptions on which he has based the diagram it is difficult to find justification for this.

(3) The ithomiines are apparently more closely related to the danaines than to the satyrines (the reverse has recently been suggested by Fox, 1956).

(4) *Bia* appears to be a typical satyrine.

(5) The subfamily Morphinæ includes all of the genera (except *Bia*) which have been previously placed in the Morphinæ, Amathusiinæ, Brassolinæ and Caliginæ. The principal basis for the previously inflated classification of these insects seems to have been their large size and their popularity with collectors. The group divides at different places on the basis of different characters, and further study is needed before a satisfactory tribal classification can be attained.

(6) As can be seen from the tree of relationships the Libytheidæ could have been considered a subfamily of the Nymphalidæ merely by lowering the level at which the branches are considered to be family stems. Equally, if

this horizontal "family line" is raised, the next entity to qualify for family status would be the Baroniinæ. Why then, since the selection of level is always somewhat arbitrary, was the line placed so that the Libytheidæ became a family while the Baroniinæ remained a subfamily? If the Libytheidæ were included in the Nymphalidæ they would form a subfamily so distinct that in order to even approximate the principle of equivalence all of the remaining nymphalids would have to be placed in the single subfamily Nymphalinæ. This would reduce the Danainæ, Satyrinæ, etc. to tribal status. Retention of the classical nymphalid subfamilies has been considered important because of the relatively large number of species in the group; thus the libytheids have not been included in the Nymphalidæ.

In the case of *Baronia* nothing could be gained by retaining a monotypic family when the genus could legitimately be included as a subfamily of the Papilionidæ. Fortunately other groups already established in the Papilionidæ were sufficiently distinct that the inclusion of the Baroniinæ did not unbalance the classification of the family. Had this not been the case the Baroniinæ would have been accorded family rank.

(7) The lycænids and riordinids were found to be so similar morphologically that there was no excuse for retaining them as separate families. The most constant difference was in the form of the male prothoracic leg. In the Riordininæ it is less than one-half the length of the prothoracic legs and has the coxa extending spine-like below the articulation of the trochanter. In the Lycæninæ the leg is more than one-half the length of the prothoracic legs, and, except in *Curetis*, there is no extension of the coxa below the trochanteral articulation.

(8) *Styx infernalis* Stgr. is definitely lycænoid in character and is placed in a monobasic subfamily of the Lycænidæ.

(9) On the basis of an analysis of 35 characters, the family Papilionidæ is the only one which appears to have significantly more characters in their specialized states than the other four families.

References

- Clark, A. H., 1948. Classification of the butterflies with the allocation of the genera occurring in North America north of Mexico. *Proc. Biol. Soc. Washington* 61: 77-84.
- Ehrlich, P. R., 1958a. The integumental anatomy of the monarch butterfly, *Danaus plexippus* L. (Lepidoptera: Danaidæ). *University of Kansas Science Bulletin* 38: 1315-1349, 41 figs.
- 1958b. The comparative morphology, phylogeny and higher classification of the butterflies (Lepidoptera: Papilionoidea). In press, *University of Kansas Science Bulletin*.
- Ford, E. B., 1944. Studies on the chemistry of pigments in the Lepidoptera, with reference to their bearing on systematics. 4. The classification of the Papilionidæ. *Trans. Roy. Ent. Soc. London* 94: 201-223.
- Fox, R. M., 1956. Monograph of the Ithomiidæ (Lepidoptera). Part 1. *Bull. Amer. Mus. Nat. Hist.* 111: 1-76, 9 pls., 75 figs.
- Michener, C. D., & R. R. Sokal, 1957. A quantitative approach to a problem in classification. *Evolution* 11: 130-162.
- Warren, B. C. S., 1947. Some principles of classification in Lepidoptera with special reference to the butterflies. *Entomologist* 80: 208-217, 235-241.