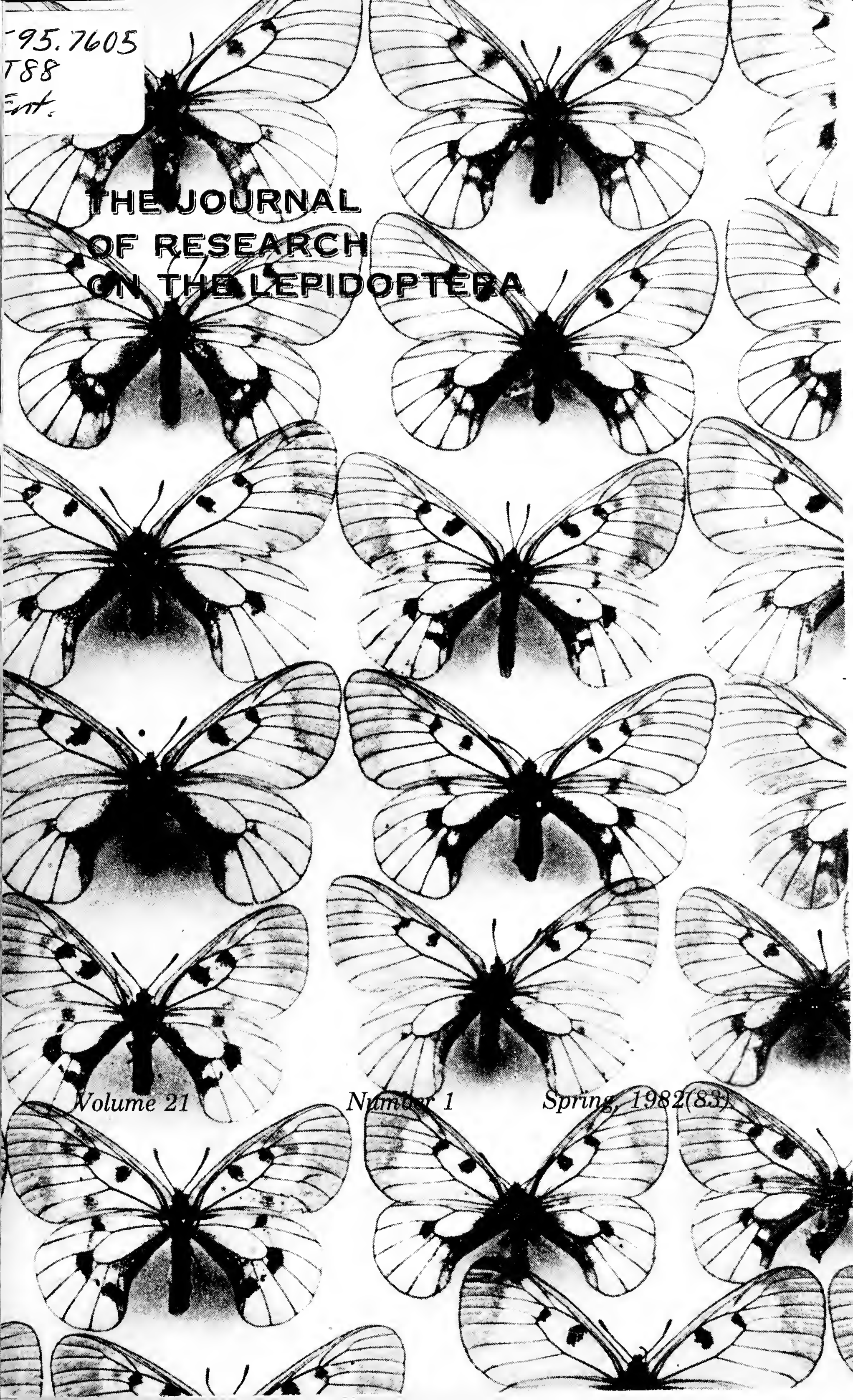

# THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

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Roger Verity, 1883-1959. A reproduction of a large hand-coloured photo made around 1937 and later bequested by Verity to the Museo Zoologico de la Specola (Firenze).

# An Annotated Catalogue of the Butterflies (Lepidoptera: Papilionoidea) Named by Roger Verity

### by Otakar Kudrna

# An Annotated Catalogue of the Butterflies (Lepidoptera: Papilionoidea) Named by Roger Verity

## *Table of Contents*

**Abstract.** R. Verity (1883-1959) named over 1,500 taxa of Holarctic (predominantly European) Papilionoidea and published 120 papers and books on the subject; his collection is deposited in Florence (Italy). The present work, based on the study of Verity's publications and his collection, attempts to review and analyse his contributions to lepidopterology to establish a basis for further taxonomic research of the butterflies.

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COVER ILLUSTRATION: Male genitalia of *E. lafontainei*, lateral view, Inuvik, N.W.T., with right valva removed, showing variation of valva shape. See Troubridge & Philip, page 136, this issue.

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## IN THIS ISSUE

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Cover Illustration: Integument sculpturing, 3rd instar larvae of *Lycaena epixanthe*. Scanning electron micrograph by David M. Wright from a forthcoming paper in Volume 22, number 1.

*Journal of Research on the Lepidoptera* 21(1): 1-106, 1982(83)

# An Annotated Catalogue of the Butterflies (Lepidoptera: Papilionoidea) Named by Roger Verity

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## Introduction

In the course of his long life Roger (Ruggero) Verity named and—usually inadequately—described some 2,000 new species-group and lower taxa of Papilionoidea, Hesperiidae and Zygaenidae mostly from Europe, but also from Palaearctic Asia and Africa, and a few from Nearctic America. This he achieved in an impressive number of over 150 publications. No serious student of Lepidoptera—whether taxonomist or not, no matter what his nationality—can ignore Verity's contributions to lepidopterology, although they usually prove to be a real stumbling block.

The aim of the present work is to provide the student of the butterflies with an annotated catalogue of the names proposed by Verity for the Holarctic Papilionoidea supplemented with an annotated bibliography of his relevant publications. Information regarding his collection, life, work, etc. is compiled in form of references to the already published materials, selected on their merits.

The results of my studies are based on the examination of all Verity's publications and type-material of the taxa concerned deposited in the Museo Zoologico de la Specola, Florence. Type-material deposited elsewhere is listed only in a few exceptional cases. The significance of type-material—the holotype (lectotype) is the only objective definition of the taxon—is increased by the fact that Verity's original descriptions are by and large very poor, confused and inadequate for precise identification, even though they usually satisfy the minimum required by the International Code of Zoological Nomenclature. Taxonomic histories are not given here. However, special attention is paid to the appearance of available names in major revisions and to some infrasubspecific names treated in selected monographs as species-group names.

Abbreviations of taxonomic categories are explained in the introduction to the catalogue. Unless otherwise stated, the types are deposited in the Museo Zoologico de la Specola, Via Romana 17, I-50125 Firenze (Italy). All periodicals and serials are abbreviated according to the *World List of Scientific Periodicals* and the *List of Serial Publications in the British Museum (Natural History) Library* (Ed. 3, 1980). The 1964 edition (Ed. 2) of the *International Code of Zoological Nomenclature* (abbreviated ICZN), with latest amendments, in addition to the draft of and comments to the third edition of ICZN, have been consulted. Numerical references to Verity's publications correspond to those heading the entries in the bibliography; page, if given, follows after colon. Data and comments placed in square brackets are my own and are intended to relate, complete or explain the original information.

It is not possible to discuss at length here Verity's views, achievements, biography or to give a comprehensive account of his collection. Biographical data of Roger Verity (born in Florence 20 May 1883, died in Florence 4 March 1959) are to be found in his publications (114, 117) and comprehensive biographies published by Baccetti (1963) and Beer (1959, 1960). The collection was described by Kudrna (1976). Since the publication of the latter report, a new type-collection of the Papilionoidea was formed, and a complete overhaul of the "rest" of the collection started. To understand some of Verity's views, study of the following publications is likely to prove beneficial: 056, 059, 061, 062; with particular attention to the following pages: 056: 118, 059:29, 061:102-103 and 062:144-147.

An interesting critical review of Verity's 'Le farfalle diurne d'Italia' (114, 115) was published by Hemming (1947). Heinrich (1925) dealt with Verity's 'racial theories' and many critical comments can be found in the *Entomologist's Rec. J. Var.*, volumes 38 and 39 (1926, 1927). Davenport (1941) gave a very interesting critical account of Verity's view on the species and lower taxonomic categories as evidenced by *Coenonympha pamphilus* (Linnaeus, 1758), with reference to 057.

Verity was above all a collector, and all his activities concentrated on his collection. He was not a very meticulous keeper, however, the best specimens usually originated from his numerous purchases of material from the dealers, mainly the Querci family and the German firm Staudinger & Bang-Haas (Dresden). Querci and his wife collected and set specimens for him for nearly all their lives.

Like many of his predecessors, Verity considered the naming of various, chiefly infrasubspecific, taxa the utmost task of lepidopterology. His school finds still today many enthusiastic followers ready to burden the already incomprehensible nomenclature of the butterflies with new, usually subspecies-rank names, for endless supposedly geographical variant populations. Like his many contemporaries, he preferred a complicated multigrade scale of taxonomic categories below species-rank. Verity explained his views on the classification of Lepidoptera on numerous occasions: 010, 018, 021, 042, 056:103, 057, 077 and 114.

Verity's species concept was rather near to the biological species concept, but applied even more inconsistently than by other authors. Verity utilized "subspecies" in his earlier works (e.g. 010), but later rejected "subspecies" (056:103), only to replace it by "exerge", the definition of which hardly differs from the former. Having made a clear distinction between the subspecies-rank (available) names and race-rank (unavailable, infrasubspecific) names in his earlier work (010), Verity (042:146, 1920) offered again an unequivocal statement to define the subspecies: 'the term "subspecies" I should restrict to particular groups of races which only just fall short of the definite group we call "species" '. The subsequent rejection of the term subspecies and its replacement with a fanciful term exerge (056:103, 1925) changed nothing on the fact that the race was a taxonomic category inferior to the subspecies/exerge-rank. This Verity (010, 018) established as early as 1911.

In 1929 Verity summarized his views on the classification and lower taxonomy as follows (077:480):

Species: 'both the hereditary factors of some features and those which control reproduction are different. [Species] can intermix, but they never interbreed or, when they do exceptionally, they only produce hybrids, which are never fertile for more than a few generations.'

Exerge: 'the hereditary factors of some features are different, but interbreeding produces perfectly fertile offsprings. [Exerges] always inhabit different land-areas, except in particular cases, such as large mountain chains and plains, which afford very different surroundings and climates within the same area; they often consist in a long chain of races [i.e. clines] stretching even from one continent to another,' [i.e. race should also be interpreted as one step in a clinal variation]; 'they fight to exclude each other' [i.e. they are allopatric] and 'The so-called "races" of Mankind are typical exerges'.

Races: [are] 'produced by the direct action of different surroundings on the development of the individuals, so that their features must fall within the limits of the elasticity allowed by the hereditary factors they have in common.'

This implies that in all polytypic species the race-rank name follows as an addition to a trinomen, i.e. Genus species exerge [i.e. subspecies] race in that order. In monotypic species the third name is left out but never replaced by the race-rank name.

Verity was quite inconsistent in naming of exerges. Although he usually applied zoological names, on many occasions he referred to the 'southern exerge', 'northern exerge' or 'central exerge'. It is impossible to incorporate this second system of denoting the exerge within the boundaries defined by the Code. Similar problems are caused also by synexerge. The complex contradictions are so great that I do not want to pretend that an instant and unequivocal solution can be found.

The 'race' is probably the most confused, and most confusing, taxonomic category in Verity's work: it has been misunderstood and misinterpreted by nearly all subsequent authors who treated names originally proposed for races as available subspecies-rank names. Two facts seem to be responsible for the confusion: the unwillingness of some authors to study the background behind the taxonomic categories, and the simple subconscious association between the race understood as a geographical form on the one hand and the subspecies as a form exclusive to and characteristic of a certain geographical area on the other.

Verity (114:XV, 1940) later specifically criticised the adoption of the term subspecies by his contemporaries for the taxonomic category he called race, on account of subspecies-rank names being accepted by the International Code of Zoological Nomenclature. Verity felt that the growing numbers of available names presented a burden and the description of subspecies in all but exceptional circumstances (cf. exerge) amounted to an abuse of the rules of zoological nomenclature.

The imminent introduction of the third edition of the ICZN is likely to bring about an alteration of the rank of some of Verity's names from infrasubspecific to subspecific. A draft of the new Code, available to me at the time of this writing, contains a redefinition of the nomenclatorial rank subspecies. The draft treats all pre-1961 names proposed originally for a "race" as of subspecific rank unless they were specifically referred to an infrasubspecific category or constituted an addition to a trinominal original combination. The acceptance of this new formulation is unlikely to give more stability to Verity's names proposed for races. A large number of names, at present deemed to be infrasubspecific, may become of subspecies-rank. Such re-ranking will be subject to the opinion of the individual subsequent revisers, and their interpretation of the original combination, which Verity so rarely stated in full. It must be remembered that Verity used a trinomen both for subraces of monotypical species (e.g. the nymphalid *Fabriciana elisa sardonia* Verity, 1950) and for individual forms particular to more than one specific race. Furthermore, the names of these forms were often applied to the race in which they were found more often, as well as the usually trinominal combinations of seasonal forms applied to the race that produced them more than others.

Names proposed originally for races and likely to become subject to the above discussed interpretation, resulting in their being treated as subspecies as from the date of their first publication after the introduction of the new ICZN, are marked with an asterisk in the catalogue. The subspecific/infrasubspecific rank of such taxa is likely to differ from one author to another unless the International Commission on Zoological

Nomenclature takes an action to stabilize their status.

It would be a pity if this catalogue, having sorted out most of the confusion surrounding Verity's names, missed the opportunity to make a positive contribution towards the stabilization of their nomenclature. The practical application of the research is the compilation here of the established original combinations and taxonomic rank of the names listed. Stabilization could only come about if the International Commission on Zoological Nomenclature were to use its plenary powers to resolve that all Verity's names included in this catalogue if listed with caption set:

**In Small Letters Without Asterisk**, are deemed as originally published in the combination and taxonomic rank stated, regardless as to whether a different original combination and/or rank may be equally well implied. These names are not to be interpreted as available species-group names as from the date stated; their subsequent elevation—regardless whether intentional or by indirect implication—to the rank of "race" or to any of the species-group categories, if made by Verity himself or together with another author, is not to be interpreted as a promotion of the name concerned to the new taxonomic rank (i.e. species or subspecies).

**In Small Letters With Asterisk** (i.e. trinominal names for "races", infrasubspecific according to Verity's wishes, and either subspecific or infrasubspecific according to the application of the abiguous Article 45 of the International Commission on Zoological Nomenclature draft), are deemed originally published in the combination listed in the catalogue and of subspecies-rank, even though this contradicts both Verity's wishes and a part of Article 45. Authors who accept the subspecies-rank of names marked with asterisk are to disregard [nec Verity] referring to the apparently first use of the name at species-group.

**In Capitals** (i.e. all species-group names) are deemed originally published in the combination and of the taxonomic rank (i.e. species or subspecies as applicable) stated in the catalogue.

Consequently, all subsequent changes of rank made by Verity himself, including the elevations of infrasubspecific names to a category of the species-group (by implication), are to be treated as null and void. Names in the latter group have often been used at the subspecific rank by subsequent authors, and a few such names are now considered distinct species. Such names are now reasonably well established, and most of them are objectively defined by primary types accessible to scientists in Florence. It is simple to conserve these names in their original combination; it is very difficult to establish their complete taxonomic histories and to establish their new primary types, bearing in mind that the identity of the taxa raised to species-group could differ in some cases from the original Verity's races listed here. It is equally convenient to place these names in synonymy in subsequent taxonomic revisions, which is probably the inevitable fate of the large majority of the species-group names proposed by Verity. Such a simple approach would contradict current day-to-day practice and may hurt the feelings of many "nomenclatorially thinking" taxonomists. Yet, it is an approach calling for reason and common sense in zoological nomenclature. Zoological nomenclature is primarily a tool to all zoologists, it being presumed universal, and is not suitable as a toy in the hands of some taxonomists. It is of secondary importance whether the currently used binomen of a species is also its valid name, as long as it is unequivocal and generally understood by all users. It would be, however, a great advantage if both the primary and the secondary aspects of zoological nomenclature could be united. With the alterations made from time to time to the ICZN, and its becoming increasingly complex, the era of common sense and reason in zoological nomenclature is yet unlikely to be imminent. It seems that some actions of International Commission on Zoological Nomenclature, and certain alterations of the ICZN in particular, are contrary to the preamble chosen to define the chief aim of this body, bringing about even Code-induced changes of names established on account of the rules introduced in an earlier edition. Consequent conservation of binomina (in their original combination, perhaps with a reference to the recommended generic name) now appears to be the only way towards stability in zoological nomenclature, but needs to be carried out rapidly on a rather massive scale. Sadly, I am inclined to believe that the self contained puristic nomenclatorial formalism—to be distinguished from the need for formal clarity expected from the taxonomists' work—grows disproportionally with the increase of our understanding biological nature and the principles of taxonomy.

It may be useful to summarize here the main points concerning Verity's concept of races. Verity was one of the first lepidopterists to observe that the general pattern of variation in the butterflies was not only geographical and attempted to establish a system of classification to reflect this. He distinguished a new taxonomic category, subordinate to the purely geographical "subspecies", utilizing the term "race" to denote the new unit. Verity's races did not necessarily include all individuals of any population of the species and/or were not necessarily exclusive of any definite territory; the taxa were believed to be phenotypes (or predominantly of phenotypic nature peculiar to and/or characteristic of specific environments. True to his principles, as naming was to him the dominant task of the taxonomist, he named as many newly discovered taxa as he believed worthy of recognition. Their names were originally intended as infrasubspecific, therefore new unavailable, but were treated as subspecies-rank names by the majority of subsequent authors. This was probably the result of Verity's unfortunate choice of the term race for the category (cf. Rasse). Owing to the widespread application of Verity's races at the subspecies-rank, it is more correct for taxonomists—and most imperative for the sake of the stability of zoological nomenclature—to treat all names originally proposed for races, if proposed in a trinominal original combination, as if they were available names originally proposed for subspecies. (These names are marked with asterisk in this catalogue.) Such an approach would exclude names proposed for seasonal or individual forms characteristic of a locality and subsequently applied to race.

The remainder of the taxonomic categories employed by Verity present no difficulties. They are infrasubspecific and the names are unavailable whether they are called subrace, seasonal form, individual form, hybrid, aberration, etc. Verity often applied one name to several infrasubspecific taxonomic categories at the same time. His attempt to divide the variation into two groups (somatic and hereditary forms) was well meant, but served no useful purpose owing to the lack of data required to classify them at the time. It was quite usual for Verity to name an individual, seasonal or other form, and subsequently apply the same name to the race where the form was particularly abundant or dominant. His so called mixed races consisted of more than one basic form.

It seems that Verity on several occasions introduced new names which he attributed to other authors; such names are not listed in this catalogue unless they have been discovered by pure chance. Also all Verity's genus-group names have been excluded from this catalogue: they have already been treated by Hemming (1967). In spite of my efforts to catalogue all names proposed by Verity and deliver a comprehensive account of them, I cannot be sure that I have fully succeeded in tracing every one.

Some now valid replacement names proposed by Verity to correct certain cases of primary homonymy may become invalid after the introduction of the third edition of ICZN, subject to the possible alterations of Art. 51.

*Acknowledgments.* It is a pleasure to express my sincere thanks to all individuals and bódies who supported my research and contributed thus to the completion of this work.

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Professor B. Lanza, Director of the Museo Zoologico La Specola (Firenze, Italy) and his staff provided me with research facilities during my reglar long-term visits to the museum, and Prof. M. Eisentrauf offered me research facilities in 1977 for the project at Zoologisches Forschungsinstitut und Museum Alexander Koenig (Bonn, Germany).

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## An Annotated List of Verity's Publications on Holarctic Papilionoidea

The following bibliography includes all papers by Roger Verity on, or related to, the Holarctic Papilionoidea (Rhopalocera). Two other bibliographies of R. Verity have been published: Beer (1960) and Baccetti (1963). They listed all papers by Verity, whether on entomology or medicine, but both failed to give at least one paper each (107). They differ from this bibliography also in other formal and factual respects. The arrangement of papers listed here is chronological, and all publications are numbered from 001 to 120 for easy reference. Some longer papers or books, published over two or more years, appear here under more than one number in order to avoid confusion between the chronology and true date of publication; all thus listed continued items are clearly cross-referenced. Verity published four papers together with other authors (015, 020, 047, 052); in two cases (015, 020 Verity was junior author (with E. Turati); in the remaining two cases Verity was senior author (with O. Querci) and retained specifically the authorship of new taxa named therein (047, 052). Comments are given on any relevant aspect of the publications included in this bibliography, especially on the dates of publication, if necessary. All accents, e.g. in titles of papers published in French, are omitted. Titles of reports from meetings are given here in square brackets. Owing to some contradicting evidence it proved impossible to establish beyond doubt the true dates of publication of Verity's papers 026, 027, 028, 029 and 030 which all appeared in Bollettino della Societa Entomologica italiana, volumes 45 and 46, due in 1913 and 1914 respectively, but published probably two years later. According to Guiglia, Magistretti & Mattioni (1969) these papers were published one year earlier than listed here. The date of publication of all taxa originally named therein may prove to be one year earlier than stated in this work.

**001**—1903—Lepidotteri Ropaloceri scoperti recentemente in Toscana.—Florentia, Rivista dell'Istituto Domenge-Rossi 1(1-2):3-10.

For English translation of this paper see item 004.

**002**—1903—Observation biologique.—Bull. Soc. ent. Fr. 1903:283.

**003**—1903—Aberrations nouvelles ou peu connues de *Lycaena icarus* Linne.—Bull. Soc. ent. Fr. 1903:287-289.

**004**—1904—New forms and new localities of some European butterflies.—Entomologist 37:53-59.

English translation of item 001.

**005**—1904—[*Lycaena icarus* and *Pieris brassicae*]. In: Adunanza del 1. Maggio 1904.—Boll. Soc. ent. ital. 36:4-6.

**006**—1904—[*Lycaena coridon* Poda ab. *stefanelli* e *Lycaena bellargus* ab. *bellargoides*.] In: Adunanza del 5. Giugno 1904.—Boll. Soc. ent. ital. 36:11-12.

**007**—1904—Elenco di Lepidotteri raccolti nell'Appennino Pistoiese (700 metri) (15 Luglio-3Settembre 1903).—Boll. Soc. ent. ital. 36:58-93.

**008**—1905—Elenco di Lepidotteri raccolti sul littorale del Lucchese (Forte dei Marmi).—Boll. Soc. ent. ital. 36(1904):123-170.

**009**—1905—Osservazioni lepidotterologiche.—Boll. Soc. ent. ital. 36(1904):185-188.

**010**—1905-1911—Rhopalocera palaearctica. [1.] Papilionidae et Pieridae.—86+368 pp., 2 + 12 + 72 pls. (many col.); publ. by the author, Firenze.

This work is part one of a planned 'Iconographie et descriptions des papillons diurnes de la region palearctique'; the plan was never realized, this being the only published volume. The systematic index to the volume was published separately and is listed here as item 018. This volume was issued over six years in installments. Dates of publication of all installments were first given by Verity (024), in an incomplete version: Verity (024) overlooked that the first installment was published in two different editions at different times. The extremely rare first edition contained no new names and its original date of publication agrees with that given by Verity in 024; the second edition contains new names and its date of publication is established here for the first time, based on Verity's handwritten note found on his working copy of 024 reprint. The second edition is best recognized from the first through a reference to p. 107 given on p. 16, which is absent from the first edition. Dates of publication of all installments are set out in a separate table (Table 1). The colour plates are very fine examples of early colour photography and also the quality of printing is of high order. Although this work is probably Verity's all time best, achieved very early in life, it suffers from inconsistencies typical for all his efforts: the same taxa are referred to different taxonomic categories and thus also different implied combinations. Nonetheless, the systematic index (pp. i-lxxxvi), an inseparable part of the book, provides all names with unequivocally stated taxonomic categories and original combinations, which are accepted also in the catalogue. The 'race' is treated also in this systematic index by Verity as infrasubspecific category, although it appears occasionally as a trinomen in monotypical species which according to his opinion have no subspecies but numerous races and individual

**Dates of Publication of the Installments of 'Rhopalocera Palaearctica'**

| Installment | Date | Pages | Plates |
|---|---|---|---|
| 1 (Ed. 1) | 30. IX. 1905 | 1 – 16 | II, III |
| 2 | 30. XI. 1905 | 17 – 24 | VI–VII |
| 3 | 31.XII.1905 | 25 – 36 | I,IV |
| 4 | 30. IV. 1906 | 37 – 52 | VIII,XII |
| 5–6 | 30. XI. 1906 | 53 – 68 | IX,XI,XIII,XV,XXI |
| 7–8 | 28. II. 1907 | 69 – 84 | XVI,XVIII,X,XX,XXII |
| 9–10 | 31. V. 1907 | 85 – 100 | XIV,XVII,XIX,XXIII |
| 11–12 | 31. X. 1907 | 101 – 124 | XXVI,XLI,XLIII,XLIV |
| 13–14 | 31. I. 1908 | 125 – 156 | XL,XLII,XLVI |
| 15–16 | 30. VI. 1908 | 157 – 172 | XXVII–XXIX,XXXIV,XLV |
| 17–20 | 30. XI. 1908 | 173 – 220 | XXX,XXXI–XXXIII,XLVII,XLIX |
| 1 (Ed. 2) | 31.XII. 1908 | 1 – 16 | ? |
| 21–23 | 30. IV. 1909 | 221 – 268 | XXXVI–XXXIX |
| 24–25 | 31.XII. 1909 | 269 – 284 | XXIV,XXXV,XLVIII |
| 26–29 | 31. I. 1911 | 285 – 324,<br>361 – 368 | LII–LIV,LVII–LXV,1–7 |
| 30–36 | 31. X.1911 | 325 – 360,<br>i–lxxxvi | XXV,L–LI,LV–LVI,LXVI–LXXII,<br>8–12,A–B, maps, gazetteer |

forms, such as *Parnassius apollo*. The 'subspecies' was utilised consistently throughout this book as a taxonomic category very different from the race.

**011**—1906—Elenco dei Lepidotteri della Vallombrosa (Appennino Toscano) (800-900 metri).—Bull. Soc. ent. ital. 38:20-51.

**012**—1909—Elenco di Lepidotteri Ropaloceri raccolti nell'Isola d'Elba.—Boll. Soc. ent. ital. 40:106-116.

**013**—1910—[*Pieris rapae* and *P. manni*]. In: Adunanza del 5. Marzo 1910.—Boll. Soc. ent. ital. 41(1909):272.

**014**—1910—Studio comparato dello sviluppo del "*Pieris manni*" L. [sic] e "*rapae*" Mayer [sic].—Boll. Soc. ent. ital. 42:131-141.

Verity transposed the authors of both species.

**015** (020) (with E. Turati)—1911—Faunula Valderiensis nell'alta valle del Gesso (Alpi Maritime).—Boll. Soc. ent. ital. 42(1910):171-265.

**016**—1911—Alcuni Lepidotteri inediti o non ancora figurati.—Boll. Soc. ent. ital. 42(1910):266-281.

**017**—1911—Races inedites de Satyridae europeens.—Bull. Soc. ent. Fr. 1911: 311-314.

**018**—1911—L'evolution et les Lepidopteres.—86 pp., 2 pls.; Roger Verity, Florence.

Pages VII-LXXXVI are identical with corresponding pages of 'Rhopalocera palaearctica' (010), the plates which are identical with the corresponding plates in 'Rhopalocera palaearctica' (010) were included apparently only in some copies.

**019**—1911—[*Apatura ilia* and other species]. In: Adunanza dell'11. Febbraio 1911.—Boll. Soc. ent. ital. 42(1910):289-290.

**020** (015) (with E. Turati)—1912—Faunula Valderiensis nell'alta valle del Gesso (Alpi Maritime).—Boll. Soc. ent. ital. 43(1911):168-236.

Continued from 015 with a list of Heterocera; only pages 231-236 relevant to Rhopalocera: 'Addenda ai Rhopalocera' and 'Correzioni'.

**021**—1912—Considerazione sulla classificazione dei Lepidotteri e loro applicazione allo studio di alcuni problemi della evoluzione.—Monitore zool. ital. 23:45-56.

**022**—1913—Revisione dei tipi Linneani dei Ropaloceri paleartici.—Boll. Soc. ent. ital. 44(1912):200-209.

**023**—1913—Revision of the Linnean types of palaearctic Rhopalocera.—J. Linn. Soc. (Zool.) 32:173-191.

This paper provided much excitement and irritated some of Verity's contemporaries; the criticism voiced at Verity at the time was only partly just (Bethune-Baker, 1913; Jordan, 1913; Wheeler, 1913, 1914). The originality of Verity's approach to systematics through the examination of the type-material was unusual at the time. Many of his observations were accurate and later confirmed by other authors; unfortunately, at least some of Verity's conclusions were exaggerated or unsubstantiated. In this paper Verity tried to establish type localities for many species named by Linnaeus and many of his conclusions have been by and large accepted. Verity replied to his critics in item 025; 023 in Italian given as 022.

**024**—1914—Dates of publication of "Rhopalocera palaearctica, Iconographie et description des papillons diurnes de la region palearctique par Roger Verity (Papilionidae et Pieridae)."—Novit. zool. 21:426.

Overview of the dates of publication of the installments of the item listed here as 010, and probably applicable also to item 018.

**025**—1914—Note in answer to Dr. Jordan's, Mr. Bethune-Baker's and the Rev. G. Wheeler's observations on my "Revision of the Linnean types of Palaearctic Rhopalocera."—Entomologist's Rec. J. Var. 26:170-176.

Verity's contribution to the discussion of his paper listed here as item 023.

**026** (035)—1915—Contributo alle richerche sull'epoca di comparsa dei Lepidotteri allo stato di completo sviluppo. [Part 1].—Boll. Soc. ent. ital. 45(1913):109-127.

**027**—1915—Elenco di Lepidotteri Ropaloceri dell'Alto Appennino Pistoiese (900-2000 m. circa).—Boll. Soc. ent. ital. 45(1913):139-154.

**028**—1915—Contributo allo studio della variazione nei Lepidotteri tratto principalmente da materiale di Toscana, delle Marche e di Calabria.—Boll. Soc. ent. ital. 45(1913):203-238.

**029**—1916—Le variazioni geografiche della "*Lycaena coridon*" Poda nell'Italia centrale.—Boll. Soc. ent. ital. 46(1914):128-133.

**030**—1916—[*Lycaena coridon*-species group]. In: Adunanza del 16. Dicembre 1916—Boll. Soc. ent. ital. 46(1914):203-204.

**031**—1916—Faunula della provincia di Macerata (Marche).—Boll. Soc. ent. ital. 47(1915):45-78.

**032**—1916—Sur deux *Lycaena confondus* sous le nom de *L. (Agriades) corydon* Poda.—Annls. Soc. ent. Fr. 84:514-520.

**033**—1916—The British races of butterflies: their relationship and nomenclature.—Entomologist's Rec. J. Var. 28:73-80, 97-102, 128-133, 165-174.

**034**—1917—Nuove osservazioni sui Lepidotteri Ropaloceri dell'Isola d'Elba.—Boll. Soc. ent. ital. 48(1916):175-192.

**035** (026, 037)—1917—Contributo alle richerche sull'epoca di comparsa dei Lepidottei allo stato di completo sviluppo. [Part 2].—Boll. Soc. ent. ital. 48(1916): 194-200.

**036**—1917—Une nouvelle methode de montage et de conservation des Lepidopteres par serie.—Bull. Soc. ent. Fr. 1917:312-316.

**037** (035)—1919—Contributo alle richerche sull'epoca di sviluppo dei Lepidotteri allo stato di complete sviluppo. [Part 3].—Boll. Soc. ent. ital. 50(1918):3-11.

**038**—1919—Le varie modalita di schiusura ed il numero di generazioni annue dei Grypocera et Rhopalocera europei illustrati dalle specie toscane di pianura e di collina.—Atti. Soc. ital. Sci. nat. 58:1-28.

English translation listed as item 039.

**039**—1919—The various modes of emergence and the number of annual broods of the Grypocera and of the Rhopalocera of southern Europe, illustrated by the Tuscan species.—Entomologist's Rec. J. Var. 31:66-72, 104-110, 141-148.

Italian translation listed as item 038.

**040**—1919—*Hyponephele lycaon,* Rott. and *H. lupinus,* Costa, two distinct species.—Entomologist's Rec. J. Var. 31:204-205.

**041**—1919—Some suggestions to Mr. Ashby on specimens collected in Italy.—Entomologist's Rec. J. Var. 31:206.

**042**—1919-1922—Seasonal polymorphism and races of some European Grypocera and Rhopalocera.—Entomologist's Rec. J. Var. 31(1919):26-31, 43-48, 87-89, 121-129, 178-184, 193-201; 32(1920):3-8, 140-152; 33(1921):170-176, 190-193, 210-214; 34(1922):12-15, 68-73, 89-93, 124-142..

**043**—1920—Pietro Stefanelli.—Boll. Soc. ent. ital. 51(1919):76-81.

**044**—1920—On emergence of the Grypocera and Rhopalocera in relation to altitude and latitude.—Entomologist's Rec. J. Var. 32:65-71, 107-110.

**045**—1920—Race francaise de *Melitaea aurelia* Nick.—Bull. Soc. ent. Fr. 1920: 272-274.

**046**—1920—Contributo alle ricerche sulla variazione e la distribuzione dei Lepidotteri in Italia: Zydaenides, Grypocera e Rhopalocera del Massiccio delle Mainarde (Prov. di Caserta).—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Protici 14:33-62.

**047** (052) (with O. Querci)—1922—Races and seasonal polymorphism of the Grypocera and Rhopalocera of Peninsular Italy.—Entomologist's Rec. J. Var. 34:154-158, 177-183, 195-200.

**048**—1922-1923—On the geographical and seasonal variations of *Pararge megera,* L.—Entomologist's Rec. J. Var. 34(1922):209-214; 35(1923):23-29.

**049**—1923—On some Italian races of *Erebia aethiops,* Esp., and of *E. pirene,* Hub. (= *stygne,* O.), and on *E. flavofasciata,* Ruhl-Heyne.—Entomologist's Rec. J. Var. 35:134-136.

**050**—1923—The nomenclature of the European *Euchloe ausonia,* Hb. (= *belia,* auct. nec L.).—Entomologist's Rec. J. Var. 35:169-171.

**051**—1923-1924—Geographical variation in *Hipparchia semele,* L.—Entomologist's Rec.J. Var. 35(1923):153-156, 209-214; 36(1924):23-29.

**052** (047) (with O. Querci)—1923-1924—Races and seasonal polymorphism of the Grypocera and of the Rhopalocera of Peninsular Italy. (Annotated list).—Entomologist's Rec. J. Var. (Suppl.) 35(1923):1-20; 36(1924):21-46.

Paper was continued from March 1923 until December 1924 as a free continuation of item 047. By implication, all new names proposed here belong to Verity. Supplemented by 053.

**053**—1924—Additions and corrections to "List of Grypocera and Rhopalocera of Peninsular Italy".—Entomologist's Rec. J. Var. 36:106-111.

A supplement of 052.

**054**—1925—Notes on Spanish Lepidoptera.—Entomologist's Rec. J. Var. 37:76.

**055**—1925—A systematic index of the races of Palaearctic Rhopalocera described by H. Fruhstorfer.—Arch. Naturgesch. (A)9:102-120.

The catalogue contains numerous nomina nuda which resulted from accepting the so called 'manuscript names' from the collection labels or an unpublished catalogue of "types" apparently deposited in the Fruhstorfer collection. These nomina nuda are usually attributed to Verity by other authors, which is probably erroneous at least in some cases. Regardless of authorship these names have not been subject to this revision, apart from a few exceptional cases.

**056**—1925-1926—Remarks on the evolution of the Zygaenae and attempts to analyse and classify the variations of *Z. lonicerae*, Scheven, and of *Z. trifolii*, Esp., and other subspecies.—Entomologist's Rec. J. Var. 37(1925):101-104, 118-121, 135-138, 154-158; 38(1926):9-12, 22-26, 57-62, 69-74.

Only the definition of taxonomic categories of species group and especially of the exerge relevant to the butterflies.

**057**—1926—The geographical and seasonal variations of *Coenonympha pamphilus* L.—Z. wiss. Insek. Biol. 21:191-208.

**058** (087)—1926-1928—Zygaenae, Grypocera and Rhopalocera of the Cottian Alps compared with other races. [1].—Entomologist's Rec. J. Var. 38(1926):101-106, 120-126, 170-176; 39(1927):122-126, 154-157, 172-175; 40(1928):142-144, 160-163.

The paper was serialized, with a gap of some four years between cross-referenced installments which appeared in vols. 40 and 44 of the journal; see also item 087.

**059**—1927—Dr. Roger Verity and nomenclature. -Entomologist's Rec. J. Var. 39:29-30.

**060**—1927—On the variations and relationship of *Coenonympha arcania*, L., and *C. gardetta*, de Prun. =*philea*, Hueb. = *satyrion*, Esp.—Entomologist's Rec. J. Var. 39:37-40, 70-74.

**061**—1927—A few words of explanation and justification.—Entomologist's Rec. J. Var. 39:100-103.

**062**—1927—On the use of names in the study of variation.—Entomologist's Rec. J. Var. 39:144-147.

**063**—1927—La variation geographique dans l'Europe occidentale des *Plebeius idas* L. (= *argus* Schiff. = *argyrognomon* Berg.) et *insularis* Leech. Le nom du *P. lycidas* est de Meigen et non de Trapp.—Annls. Soc. ent. Fr. 96:1-16.

**064**—1927—Notes sur quelques Rhopaloceres d'Espagne.—Bull. Soc. ent. Fr. 1927:172-176.

**065**—1927—Les *Agriades albicans* H.-S., *A. arragonensis* Gerh. et *A. hispana* H.-S. constituent probablement une unite specifique.—Bull. Soc. ent. Fr. 1927:205-208.

**066**—1928—Races palearctiques de Grypoceres et de Rhopaloceres a distinguer et homonymes a remplacer.—Bull. Soc. ent. Fr. 1928:140-144.

**067**—1928—Distinction de quelques races de l'*Aricia medon* Huefn. et de l'espece differente *A. cramera* Ersch.—Bull. Soc. ent. Fr. 1928:179-183.

**068**—1928—An essay on the origins of the geographical variations of the Rhopalocera in Europe exemplified by *Melitaea aurinia*, Rott.—Entomologist's Rec. J. Var. 40:41-45, 86-91, 97-101.

**069**—1929—The Asiatic origins of the western Palaearctic Rhopalocera exemplified by *Melitaea didyma*, Esp.—Entomologist's Rec. J. Var. 41:31-34, 39-43, 63-

67, 72-76, 89-91, 111-118, 127-132.

**070**—1929—Considerations sur les races francaises de l'*Heodes virgaureae* L.—Bull. Soc. ent. Fr. 1929:128-131.

**071**—1929—Races du midi de la France des *Agriades escheri* Hb. et *coridon* Poda.—Bull. Soc. ent. Fr. 1919:156-160.

**072**—1929—Remarques sur *Coenonympha dorus* Esp. et *Hyponephele lycaon* Rott. et sur l'usage incorrect du nom de *Pararge hiera* F.—Bull. Soc. ent. Fr. 1929:185-188.

**073**—1929—Les races de la France du *Nytha arethusa* Schiff.—Bull. Soc. ent. Fr. 1929:197-200.

**074**—1929—Des races europeennes de l'*Argynnis niobe* L.—Bull. Soc. ent. Fr. 1929:240-244.

**075**—1929—Races de l'Europe occidentale de l'*Argynnis phryxa* Bergstr. qu'on nomme, a tort, *adippe* L.—Bull. Soc. ent. Fr. 1929:277-280.

**076**—1929—Essai sur les origines des Rhopaloceres europeens et mediterraneens et particulierement des Anthocharidi et des Lycaenidi du groupe d'*agestis* Schiff.—Annls. Soc. ent. Fr. 98:323-360.

**077**—1929—On the necessity of a revision of the rules of entomological nomenclature concerning groups of lower rank than the specific one.—Int. Congr. Ent. (4)2(1928):479-480.

**078**—1930—Notes on the relationship between the Melitaeidi and particularly between those of the *athalia*, Rott., group.—Entomologist's Rec. J. Var. 42:29-31, 40-44, 51-54, 71-75, 81-85, 108-111, 117-120, 131-135.

**079**—1930—According to the rules of nomenclature the name of *Argynnis adippe* is of Rottemburg (nec L.), and that of *Melitaea dictynna*, Esp., must be replaced by *diamina*, Lang.—Entomologist's Rec. J. Var. 42:149-152.

**080**—1930—Communication au sujet d'*Argynnis adippe*.—Lambillionea 30: 102-104.

**081**—1931—On the geographical variations and the evolution of *Lycaeides argus* L.—Dt. ent. Z. Iris 45:30-69.

**082**—1931—Classification of the geographical variations of *Melitaea diamina*, Lang. (= *dictynna*, Esp.).—Entomologist's Rec. J. Var. 43:66-70, 80-81.

**083**—1931-1932—The specific names and the geographical variation of *Melitaea parthenoides*, Kef. (= *parthenie*, auct. nec. Borkh.) and of *parthenie*, Borkh. (= *aurelia*, Nickerl).—Entomologist's Rec. J. Var. 43(1931):100-105, 136-140, 151-155, 186-189; 44(1932):27-30.

**084**—1932—Notes on the geographical variations and the evolution of *Boloria pales* Schiff.—Dt. ent. Z. Iris 46:101-109.

**085**—1932—*Melitaea pacifica*, a species hiterto confused with *M. britomartis* form *plotina*, Bremer.—Entomologist's Rec. J. Var. 44:70-72.

**086**—1932—The geographical variations of *Boloria euphrosyne*, L.—Entomologist's Rec. J. Var. 44:110-115, 119-121.

**087** (058)—1932-1933—Zygaenae, Grypocera and Rhopalocera of the Cottian Alps compared with other races. [2].—Entomologist's Rec. J. Var. 44(1932):139-142; 45(1933):90-93, 106-109, 123-126.

Serialization of item 058 continued after a gap of some four years.

**088**—1933—The geographical and seasonal variations of *Argynnis (Issoria) lathonia,* L.—Entomologist's Rec. J. Var. 45:56-60.

**089**—1933—Notes on the geographical variations of *Argynnis niobe*, L.—Entomologist 66:243-244.

**090**—1933—Des variations geographiques et saisonnieres du *Boloria dia* L.—Bull. Soc. ent. Fr. 1933:74-77.

**091**—1933—Des Variations geographiques et saisonnieres du *Boloria selene* Schiff.—Bull. Soc. ent. Fr. 1933:116-118.

**092**—1933—Les races occidentales de l'*Argynnis hecate* Schiff.—Bull. Soc. ent. Fr. 1933:173-176.

**093**—1934—Notes on the geographical variations of *Argyronome paphia*, L.—Entomologist 67:78-80.

**094**—1934-1936—The lowland races of butterflies of the upper Rhone Valley.—Entomologist's Rec. J. Var. (Suppl.) 46(1934):1-40; 47(1935):41-76; 48(1936): 77-90.

Pagination of paper continues throughout regardless of the volume of the journal, usually four pages published at a time at end of most issues.

**095**—1935—Notes on the geographical variations of *Argynnis aglaja*, L.—Entomologist 68:189-191, 200-204.

**096**—1935—Races de *Lysandra thersites* Chapm. et de *Plebeius sephyrus* Friv. de le'Asie Mineure.—Bull. Soc. ent. Fr. 1935:243-245.

**097**—1935—Des noms de *Lycaeides idas* L. (= *argyrognomon* auct. nec. Bergstr.) et *argyrognomon* Bergstr.—Lambillionea 35:215-221.

**098**—1936—*Lysandra corona,* a new "blue" from Persia.—Entomologist's Rec. J. Var. 48:106-107.

**099**—1936—*Polyommatus parameleager,* another "blue" from Persia.—Entomologist's Rec. J. Var. 48:130.

**100**—1936—The male genital armature of *Aglais urticae* L., in connection with its variations and its phylogeny.—Festschrift zum 60. Geburtstage von Professor Dr. Embrik Strand 1:461-482; Riga.

**101**—1936-1937—The butterfly races of Macedonia.—Entomologist's Rec. J. Var. (Suppl.) 48(1936):1-8; 49(1937):9-22.

Pagination of paper continues throughout regardless of volume.

**102**—1937—Variations of *Eumenis allionii,* G.-H. = *fatua,* Freyer.—Entomologist's Rec. J. Var. 49:99-101.

**103**—1937—Des variations geographiques de l'*Eumenis briseis* L.—Lambillionea 37:4-14, 50-63.

**104** (105)—1937—Classement et distribution des races, ou formes geographiques,

du *Pyronia tithonus* L.—Lambillionea 37:221-232.
Correction to this paper listed as item 105.

**105** (104)—1937—Classement et distribution des races ou formes geographiques, du *Pyronia tithonus* L. Rectification.—Lambillionea 37:247.
Correction to item 104.

**106**—1937—Appunti su alcuni Lepidotteri diurni italiani.—Memorie Soc. ent. ital. 16:37-50.

**107**—1937—New Finnish race of *Scolitantides orion*, Pall., compared with the others of the species.—Entomologist's Rec. J. Var. 49:71-73.
This paper was not listed by any of the two previously published bibliographies (Beer, 1960; Baccetti, 1963).

**108**—1937-1938—Variation of some butterflies in Anterior Asia and in Morocco.—Entomologist's Rec. J. Var. (Suppl.) 49(1937):1-8; 50(1938):9-15.
Paper paginated throughout regardless of volume at end of issues, mostly four pages published at a time in November and December 1937 and in May and June 1938.

**109**—1938-1939—Supplement to the "Butterfly races and Zygaenae of Macedonia".—Entomologist's Rec. J. Var. (Suppl.) 50(1938):1-16; 51(1939):17-20.
Paper paginated throughout regardless of volume, at end of most issues between July 1938 and January 1939, usually four pages published at a time; colour plate published as plate 3 of volume 50 in 1938.

**110**—1939—*Parnassius apollo* L. race *romeii* nom. nov., des Abruzzes.—Lambillionea 39:181-183.

**111**—1939—Race persane du *Palaeoloweia tityrus* Poda, 1761 = *dorilas* Hufnagel, 1766.—Lambillionea 39:184-186.

**112**—1939—Essai sur la distinction des especes du groupe de *Lysandra coridon* Poda.—Lambillionea 39:210-222.

**113**—1940—Revision of the *athalia* group of the genus *Melitaea* Fabricius, 1807.—Trans. R. ent. Soc. Lond. 89:591-706.
Publications contain at end four short notes by F. Hemming, mostly on nomenclatorial subjects or of methodical nature.

**114** (115, 117, 118, 120)—1940—Le farfalle diurne d'Italia. 1. Considerazioni generali. Superfamiglia Hesperides.—34 + 131 pp., 4 col. pls., 2 pls.; Marzocco, Firenze.
The first of a five volume monograph of the butterflies and skippers of Italy. Unpublished manuscript of an English translation of selected parts from volumes 1-3 available at the Royal Entomological Society of London. Pages of the text volumes of this work numbered separately in each volume, black-and-white and colour plates numbered throughout the work regardless of volume. See also comment to item 120.

**115** (114, 117, 118, 120)—1943—Le farfalle diurne d'Italia. 2. Divisione Lycaenida.—12 + 401 pp., 15 col. pls., 6 pls.; Marzocco, Firenze.
Second part of the five volume work, see also comment to item 114.

**116**—1947-1957—Les variations geographiques et saisonnieres des papillons diurnes en France. 1-3.—472 pp.; Le Charles, Paris.
Verity never finished this work. Published in three volumes and paginated throughout regardless of volume. Later a reprint of the first edition was published, with additional

index of scientific names provided at end with pages numbered in Roman numerals. Publication dates of individual installments according to the publishers run as follows: pages 1-16 published on 23 June 1947, pages 17-64 on 10 July 1948, pages 65-96 and 97-128 on 30 September 1948, pages 129-160 on 12 February 1949, pages 161-199 on 28 June 1951, pages 201-311 on 14 March 1952, pages 313-364 on 30 April 1952 and pages 365-472 on 21 September 1957.

**117** (114, 115, 118, 120)—1947, 1950—Le farfalle diurne d'Italia. 3. Divisione Papilonida. Famiglie Papilionidae e Pieridae.—16 + 381 pp., 13 col. pls., 5 pls.; Marzocco, Firenze.

Third part of a five volume work, see also comment to item 14. Plates (col. pls. 20 - 37 and black-and-white pls. X-XIV) apparently appeared as late as 1950 while the text was available in December 1947.

**118** (114, 115, 117, 120)—1950, 1951—Le farfalle diurne d'Italia. 4. Divisione Papilionida. Sezione Libytheina, Danaina e Nymphalina.—24 + 380 pp., 16 col. pls., 1 + 6 pls.; Marzocco, Firenze.

Fourth part of five volume work, see also comment to item 114. Text was apparently published in 1950, plates (col. pls. 38-53, black-and-white plates 54 and XV-XX) appeared as late as 1951.

**119**—1953—On the supposed discoveries of new butterfly species in Europe.—Entomologist 86:172-175.

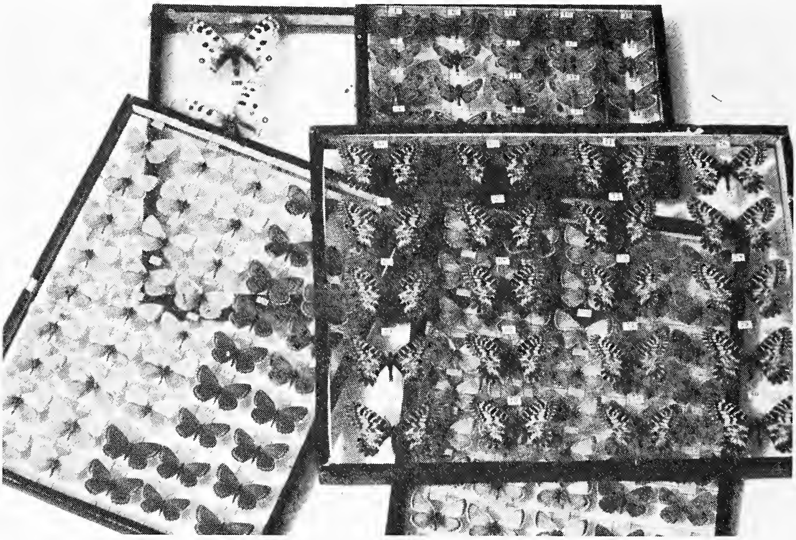
This paper was published in the July issue of the journal although the text contained reference to the later published item 120 as if it were available at the time.

**120** (114, 115, 117, 118)—1953—Le farfalle diurne d'Italia. 5. Divisione Papilionida. Sezione Nymphalina. Famiglia Satyridae.—18 + 354 pp., 20 col. pls., 6 pls.;—Marzocco, Firenze.

The last part of a five volume work, apparently published in December 1953. See also comment to item 114. Consistently through all five volumes Verity used first name Ruggero instead of its usual English form Roger used regularly elsewhere. Col. pls. numbered 55-74.

## An Annotated List of Holarctic Papilionoidea named by Verity

Families are arranged according to Verity's 'Le farfalle diurne d'Italia' (115, 117, 118, 120): Lycaenidae, Riodinidae, Papilionidae, Pieridae, Libytheidae, Nymphalidae, Satyridae. Within each family entries are arranged alphabetically, with the following standard pattern of data: name of taxon (given in CAPITALS for available names and in lower case for unavailable names, preceded by an asterisk if they could become available as from their original date of publication subject to the altered interpretation of the "race" by the ICZN, Ed. 3, Art. 45, as outlined in the preliminary draft dated 1977, regardless of the potential contradiction between two of the criteria of the definition of availability: Art. 45/f/ii and 45/f/iv)—taxonomic categroy in parenthesis, abbreviated—original combination—author(s) and year—bibliographical reference consisting of number of item as given in the annotated list of Verity's publication and the page—type-material (if found) or type-locality (if known)—comments and/or references to the taxonomic history. Authors who decide to follow my recommendation regarding the availability and subspecies-rank of "races" marked with asterisk (cf. Introduction) before the taxonomic status of these names will have been definitively settled by theInternational Commission on Zoological Nomenclature, should consequently disregard the [nec Verity] inserted after the combination used by the apparently first subsequent author who decided to treat the name concerned as if already available. Taxonomic categories are abbreviated as follows: sp = species, ssp = subspecies, nn = nomen novum, ra = race, sr = subrace, sf = seasonal form, hy = hybrid, if = individual form (s.l.), fm = form/morph (used only for names published in 010), ab = aberration (used only for names published in 010). As Verity rarely stated unequivocal original combinations these are based on judgment and various implications; it must be understood that he often proposed (by mplication) infrasubspecific names in a trinomen. Type-material is listed according to the data on specimens' labels which have been "joined" in order to save place; all parts inserted in square brackets are my own supplements intended to relate or complete the original data. The type concept follows strictly that set out by the definitions contained in the ICZN for all available names, holotypes of some certainly infrasubspecific taxa (e.g. individual forms) are often accepted without specific original designations if the taxon is believed to have been apparently described from a single specimen, allotypes are not recognized and are therefore always interpreted as paratypes. Lectotypes are not designated here as the selection of the specimens is better left to the future revisers of the groups concerned and routine selection of lectotypes is thought to be beyond the scope of this project. Since Verity was never very meticulous and consistent in labelling of type-material, many a type-series had to be reconstructed according to the implications available. Particular reference is given to the specimens removed from the so called glass cases (036) which have been carefully deep-frozen to save them from museum pests, opened, each specimen mounted on a pin and relabelled as necessary.



Examples of the "glass cases" from the Verity collection as referred to in the text.

## LYCAENIDAE

***abetonica** (ra)—*Lycaena argus abetonica* Verity, 1911—016:273—Syntypes 4♂♂, 2♀♀ [Italy: Toscana: Appennino Toscano]: Abetone: [1400 m]: 14-20 VIII [19]11: [Verity leg.].

**acaciaeformis** (if)—*Thecla ilicis inornata acaciaeformis* Verity, 1915—028:229—Italy: Firenze.

**aegusella** (ra)—*Plebeius insularis aegusella* Verity, 1921—042:175—Syntypes 2♂♂, 1♀ [Czechoslovakia]: Moravia: [Mikulov]: Pollauer B[erge]: Sterzl [leg.].

**aestivacaudata** (if)—*Lycaena phaleas aestivacaudata* Verity, 1943—115:55—Italy: Alpi Marittime: Valdieri.

**agraphomena** (if)—*Lycaena damon agraphomena* Verity, 1904—004:59—Holotype ♂ Francia: Giura: Gr. Saleve: VII [1]902; type: *agraphomena*.

**agraphomena** (if)—*Aricia nicias agraphomena* Verity, 1943—115:215.

**albata** (if)—*Glaucopsyche alexis albata* Verity, 1943—115:131—Holotype ♂ [Italy]: Firenze: Pian di Mugnone: 26 V [19]29: Verity [leg.].

**albinos** (if)—*Polyommatus icarus albinos* Verity, 1903—003:288—Holotype ♂ [Italy]: Firenze: Giogili Collazzi: 300 m: 10 VI 1903; type: *albinos*.

**albobsoleta** (if)—*Strymon pruni albobsoleta* Verity, 1943—115:373.

**alborecessa** (if)—*Strymon esculi alborecessa* Verity, 1943—115:354.

**albopraemargine** (if)—*Agriades glandon albopraemargine* Verity, 1943—115:224.

**alineata** (if)—*Thecla ilicis alineata* Verity, 1919—042:47.

**alpina** (if)—*Lycaena alexis alpina* Turati & Verity, 1911—015:260—Syntypes 1♂, 1♀ [Italy: Alpi Marittime[: Valdieri: 23 VII [19]09, VIII [18]98—Original rank: 'forma nova'; status uncertain, probably infrasubspecific name; see also *maritimalpium*.

***alpium** (ra)—*Polyommatus meleager alpium* Verity, 1926—058:120—Syntypes 4♂♂, 5♀♀ [N. italy: Torino[: Alpi Cozie: Val Susa: Oulx [= Ulzio]: 110 m: 3-11 VIII 1925: Verity [leg.]; possibly also additional 2♂♂, 2♀♀ [Switzerland]: Vallese [= Wallis]: Wulfschlegel [leg.] belong to the type-series.

***alpiumclara** (ra)—*Polyommatus meleager alpiumclara* Verity, 1926—058:121—Syntype 1♂ [Italy]: Südtirol: 191[?]; type: *alpiumclara*; possibly described from a single specimen.

***alpiumfusca** (ra)—*Agriades coridon alpiumfusca* Verity, 1926—058:125—Syntypes 2♂♂, 1♀ [Austria]: Innsbruck: Sistrans: 1000 m: 16 VII [19]20.

***alpiummagna** (ra)—*Aricia agestis alpiummagna* Verity, 1943—115:213—Syntypes 14♂♂, 3♀♀ [Italy]: Alpi Marittime: Terme di Valdieri: [1400 m]: 27 VII-20 VIII [19]09, 27 VII [19]11, 3-16 VIII [19]38: Verity [leg.].

***alpiumpallida** (ra)—*Agriades coridon alpiumpallida* Verity, 1926—058:123—Syntypes 34♂♂, 1♀ [Italy]: Südtirol: [Bozen: Eisacktal]: Chiusa [= Klausen], Waidbruck: 191[?].

**alpiumphilonome** (sr, sf, ra)—*Lycaeides argus alpiumphilonome* Verity, 1931—081:58—Syntype 1♂ Italia settentrionale: Alto Adige [= Südtirol]: Waidbruck: 25 VII [????]; rest of type-series destroyed by museum pests.

***alpophila** (ra)—*Plebeius argus alpophila* Verity, 1919—042:46—Italy: Toscana:

mountain levels—Original designation uncertain.

**altaegidion** (nn)—*Lycaeides argus altaegidion* Verity, 1931—081:59—Replacement name for apparently unavailable infrasubspecific name [*Lycaena*] *argus alpina* Courvoisier, 1910, which was proposed without generic name to denote individual form, said to be preoccupied.

**altera** (sf)—*Lycaena aragonensis rezniceki altera* Verity, 1916—032:517—Italy: Toscana.

***altivolans** (ra)—*Agriades escheri altivolans* Verity, 1920—042:144—Syntypes 2♂♂, 3♀♀ Italia centrale: Firenze: Firenzuola: 500-1000 m: 25-26 VI 1916, 9 VII 1917, 14-17 VII 1917: Querci, Verity [leg.].

***angulosa** (ra)—*Cupido sebrus angulosa* Verity, 1919—042:47—Syntypes 1♂, 3♀♀ Italia centrale: Piceno: Massiccio Sibillini: Bolognola: 1200-1600 m: 18-23 VII 1918: Querci [leg.].

**antealcetas** (sf)—*Everes alcetas alcetas antealcetas* Verity, 1934—094:34—Switzerland: Wallis: Martigny: Batiaz; described from a single specimen subsequently destroyed by museum pests—Beuret (1957): *Everes alcetas antealcetas* [nec Verity], subspecies.

**antearentior** (sf)—*Lysandra bellargus antearentior* Verity, 1937—108:5—Syntypes 26♂♂, 3♀♀ [Turkey]: Asia Minor: Sultan Dagh: 16-31 V [1930], Ak-Chehir: 1-10 VI [19]28, 16 V-15 VI [1930]: [all] Coll. Wagner, Wien.

**antebritannorum** (sf)—*Lysandra bellargus britannorum antebritannorum* Verity, 1934—094:30—Syntypes 5♂♂, 1♀ [England]: Kent: Cuxton: 16 VI [19]06: Conquest [leg.].

**antecaelestis** (sf)—*Lysandra bellargus caelestis antecaelestis*, Verity 1934—094:30—Syntypes 6♂♂, 2♀♀ [France]: Vendee: Auzay: 19 V-18 VI 1919, 24 V 1920.

**antecalida** (sf)—*Aricia agestis calida antecalida* Verity, 1943—115:209—Syntypes 14♂♂, 2♀♀ [Italy]: Isola di Sicilia: Palermo: Monreale: San Martino: 800 m: 24 IV-22 V 1918, Castronuovo: 20 V 1928: [all] Querci [leg.].

**antecimon** (sf)—*Cyaniris semiargus cimon antecimon* Verity, 1943—115:236—Syntypes 6♂♂ Italia centrale: Firenze: Pian di Mugnone: 200 m: 24 V 1918, 14 V 1919, 22 V 1920, 6-8 VI 1935: Querci, Verity [leg.].

**anteparvaplumbea** (sf, ra)—*Lysandra argester parvaplumbea anteparvaplumbea*, Verity 1934—094:28—Syntypes 2♂♂ [Switzerland: Wallis]: Martigny: 10 VII 1933: Verity [leg.].

**anteschiffermuelleri** (sf)—*Turanana baton vicrama schiffermuelleri anteschiffermuelleri* Verity, 1936—101:5—Syntypes 4♂♂, 12♀♀ [Greence]: Macedonia: Salonika: 1000 ft.: 8-31 V 1935: Romei [leg.].

**antetuscanica** (sf)—*Plebejus argus tuscanica antetuscanica* Verity, 1943—115: 189—Syntypes 10♂♂ [Italy: Toscana]: Firenze: Pian di Mugnone: 2 VI [19]29, 6-8 VI [19]35, 25 VII [19]36, 8 VI 1939: 30 V 1941, 14 VI [19]28, Fiesole: Monte Senario: 12 VII 1918: [all] Verity [leg.].

**anticoalbocincta** (if)—*Lysandra escheri anticoalbocincta* Verity, 1943—115:270.

**anticodiscoelongata** (if)—*Agrodiaetus dolus anticodiscoelongata* Verity, 1943—115:323.

**anticoelunata** (if)—*Polyommatus icarus anticoelunata* Verity, 1943—115:247.

**anticofulvomaculata** (if)—*Strymon spini anticofulvomaculata* Verity, 1943—115:364—Italy: Abruzzi: Gran Sasso.

**apenninicola** (nomen nudum)—*Agriades thetis apenninicola* Verity, 1919—042:29—Name for race published without description, definition or indication (in subheading of a paragraph).

***apenninicola** (ra)—*Plebeius argus apenninicola* Verity, 1919—042:45—Syntypes 4♂♂, 4♀♀ Italia centrale: Lucca: Prato Fiorito: 1000 m: 28 VII-7 VIII 1915: Querci [leg.].

***apenninigena** (ra)—*Agriades thetis apenninigena* Verity, 1919—042:30—Syntypes 8♂♂, 5♀♀ Italia centrale: Piceno: Massiccio Sibillini: Bolognola: 1200-1600 m: 8 VII-10 VIII 1918: Querci [leg.].

***apenninogenita** (ra)—*Agriades amandus apenninogenita* Verity, 1921—042:190—Syntypes 5♂♂, 2♀♀ Italia centrale: Piceno: Monti Sibillini: Bolognola: 1200-1600: 16 VI-11 VII 1913, 30 VI-18 VII 1918: Querci [leg.].

***apenninophila** (ra)—*Plebeius idas apenninophila* Verity, 1919—042:46—Syntypes 19♂♂, 17♀♀ [Italy: Toscana: Lucca]: Bagni di Lucca: Valle del fiume Fegana: 9-15 VIII 1915: Querci [leg.].

***apuana** (ra)—*Lysandra coridon apuana* Verity, 1916—029:131—Syntypes 4♂♂, 2♀♀ [Italy: Toscana]: Alpi Apuane: Monte Matana: VIII [19]02, VII [19]03: [Verity leg.].

**apuanica** (nomen nudum)—*Lycaena corydon apuanica* Verity, 1916—032:515—Name for race published without description, definition or indication; probably incorrect subsequent spelling *Lysandra coridon apuana* Verity 1916.

**arcuata** (if)—*Lycaena corydon arcuata* Verity, 1911—016:276—Syntype 1♂ [Italy: Toscana]: Firenze: [Pian di Mugnone]: 200 m: V [19]10: Verity [leg.].

**arens** (sf)—*Lysandra bellargus arens* Verity, 1937—108:4—Syntypes 4♂♂, 1♀ [Turkey]: Asia Minor: Malatya: Tecde: 26 V [???].

**arentior** (ra, sf)—*Lysandra bellargus arentior* Verity, 1937—108:5—Syntypes 1♂, 2♀♀ [Turkey]: Asia Minor: Erdschius-Gebiet: [Erias-dagh]: [19]02: Pentker.

**arentissima** (ra, sf)—*Lysandra bellargus arentissima* Verity, 1937—108:4—Syntypes 14♂♂, 2♀♀ [Turkey]: Asia Minor: Malatya: Tecde: 24 VII-4 VIII [????], 4 X [????].

**argigas** (ra, sf)—*Lycaeides argus argygas* Verity, 1931—081:47—Italy: Trieste: Carso: spring specimens; syntypes, probably two specimens only, now probably destroyed by museum pests.

**arida** (sf)—*Plebeius idas nocensis arida* Verity, 1927—063:9—Syntypes 5♂♂, 3♀♀ Italia settentrionale: Alto Adige [= Südtirol]: Eisacktal: Atzwang: 30 VII [19]20.

***aridogenita** (ra)—*Aricia cramera aridogenita* Verity, 1928—067:183—Syntypes 68♂♂, 25♀♀ Portugal: Serra da Estrela: [Covilha]: 800-1000 m: 13 VI-3 X 1927; [Spain]: Nueva Castille: Cuenca: Huelamo: 1200 m: 9 IX 1926, Villacabras: 1200 m: 1-16 IX 1926; [all] Querci [leg.].

**atavica** (if)—*Syntarucus pirithous atavica* Verity, 1943—115:80—Holotype ♂ [Italy: Toscana]: Firenze: [illegible]: V [1]904: [Verity leg.].

**atrescens** (if)—*Agriades coridon atrescens* Verity, 1926—058:124—Holotype ♂ [Italy: Torino]: Alpi Cozie: Val Susa: Oulx [= Ulzio]: 1100 M: 2 VIII 1925: Verity [leg.].

**AUSONIA** (ssp)—*Lycaena damon ausonia* Verity, 1915—028:232—Syntypes 10♂♂, 6♀♀ Italia centrale: Piceno: Massiccio Sibillini: Bolognola, Dintorni di Bolognola: 1200-1400 m: VIII 1912, 29 VII-30 VIII 1913: Querci [leg.]—Treated as subspecies by implication.

***ausonidarum** (ra)—*Cyaniris semiargus ausonidarum* Verity, 1919—042:5—Syntypes 1♂, 1♀ Italia centrale: [Campania]: Caserta: Monti Aureunci: Polleca: 700 m: 21-30 V 1910: Martes [leg.]; Monti Aurunci: Valle di Petrella: 1400 m: 27 VI 1911: [Querci leg.].

***austera** (ra)—*Lycaeides argus austera* Verity, 1931—081:69—Syntypes 3♂♂ [Italy]: Lago Maggiore: Intra: Pian Quaggier: 950 m: 18 VI 1922: Verity [leg.].

***australissima** (ra)—*Plebeius idas australissima* Verity, 1919—042:46—Syntypes 5♂♂, 5♀♀ Italia centrale: Toscana: Lucca: Forte dei Marmi: 2 m: 1-15, 24-31 VIII 1917, 2-22 VIII [1]900, 1 IX [19]01, 15 IX [1]903, VIII-IX [1]904, VIII [19]08: Querci, [Verity leg.].

***australpina** (ra)—*Lycaena arion australpina* Verity, 1924—053:109—Syntypes 8♂♂ Italia centrale: Piceno: Monti Sibillini: 1200-2000 m: 30 VI-19 VII 1918, Faggeti di Bolognola: 1400 m: 10-11 VI 1913; [all] Querci [leg.].

**autumna** (sf)—*Lysandra thersites meridiana autumna* Verity, 1943—115:266—Syntypes 3♂♂, 3 ♀♀ [Italy: Toscana]: Firenze: Pian di Mugnone: 7 X [19]28, 8 X [19]26, 22 X [19]40, 27 X [19]25: Verity [leg.].

**basipunctata** (if)—*Lycaena hylas basipunctata* Turati & Verity, 1911—015:257—Holotype ♂ [Italy: Alpi Marittime]: Valdieri: 10 VIII [19]09: [Verity leg.]; type: *basipunctata.*

**beccarii** (if)—*Thecla acaciae beccarii* Verity, 1904—004:56—Holotype ♂ [Italy: Toscana]: Firenze: Mt. Senario: VII 1902: [Beccari leg.].

**bellargoides** (if)—*Lycaena ballargus bellargoides* Verity, 1904—006:11—Italy.

***britanna** (ra)—*Lycaenopsis argiolus britanna* Verity, 1919—042:46—Syntypes 3♂, 7♀♀ [England: London]: Epping Forest: Woodford: 7-9 V 1876, 12 V [19]01: Conquest [leg.].

***britannorum** (ra)—*Agriades thetis britannorum* Verity, 1919—042:29—Syntypes 9♂♂, 1♀ [England]: Kent: Caxton: 26 VIII [19]05: Conquest [leg.].

***bruttia** (ra)—*Agriades amandus bruttia* Verity, 1921—042:190—Syntypes 8♂♂, 1♀ [Italy]: Costiera Calabra: Cosenza: San Fili: 570-900 m: 21-26 V 1920: Querci [leg.].

***caelestissima** (ra)—*Agriades coridon caelestissima* Verity, 1921—042:191—Syntypes 5♂♂, 1♀ Spain: [Teruel]: Albarracin, Tragacete: 28 VII-6 VIII [19]01: T. A. C[hapman leg.]—Agenjo (1956): *Plebejus (Lysandra) coridon caelestissima* [nec Verity]; subspecies.

**caeruleolineata** (if)—*Lysandra bellargus caeruleolineata* Verity, 1943—115:289.

**caeruleonivescens** (if)—*Agriades dorylas caeruleonivescens* Verity, 1927—065: 206—Spain: Cuenca: Huelamo.

**caeruleosignata** (if)—*Aricia agestis caeruleosignata* Verity, 1943—115:106.

**CAERULEOSSMAR** (ssp)—*Lysandra coridon caeruleossmar* Verity, 1939—112: 217—Syntype ♂ [U.S.S.R.]: Caucaso: [Latpari and other localities]: 2000-3000 m:

1890; probably described from a single specimen damaged almost beyond recognition—Original rank: geographical form, treated as subspecies by implication.

***calabrica** (ra)—*Plebeius argus calabrica* Verity, 1919—042:45—Syntypes 4♂♂, 6♀♀ Italia merid. Calabria: Aspromonte: 1200-1300 m: 13-24 VII 1914: Querci [leg.].

***calabricola** (ra)—*Plebeius insularis calabricola* Verity, 1921—042:175—Syntypes 8♂♂, 6♀♀ [italy: Calabria]: Costiera Calabra: Cosenza: Catena: San Fili: 900 m: 17-27 VI 1920: Querci [leg.].

**calabrus** (sr)—*Chrysophanus alciphron gordius calabrus* Verity, 1915—028:229—Syntypes 1♂, 7♀♀ Italia merid.: Calabria: Aspromonte: 1200 m: 18-29 VII 1914: Querci [leg.].

**calidogenita** (sf)—*Lycaenopsis argiolus calidogenita* Verity, 1919—042:46—Syntypes 1♂, 1♀ Italia centrale: Toscana: Firenze: Pian di Mugnone: 200 m: 1 IV 1917; Firenze: Fiesole: Monte Fanna: 650 m: 15 V 1917: Querci [leg.]—Manley & Allcard (1970): *Celastrina argiolus calidogenita* [nec Verity], subspecies.

***calliopides** (ra)—*Plebeius idas calliopis callipides* Verity, 1919—042:46—Beuret (1961): *Lycaeides idas calliopides* [nec Verity], subspecies.

**canicularis** (sf)—*Lycaenopsis argiolus canicularis* Verity, 1919—042:46—Syntypes 7♂♂, 3♀♀ Italia centrale: Toscana: Colline di Firenze: 400 m: 24 VI-5 VII 1914: Querci [leg.].

***catherinei** (ra)—*Heodes tityrus catherinei* Verity, 1948—116:58—Syntypes 1♂, 3♀♀ [France: Hautes-Pyrenees]: Val d'Heas: [1500 m]: 16 VII 1915, Cauteretes: [Lac de Gaube]: 1800 m: 29 VII 1913, VIII 1910.

***centralitaliae** (ra)—*Thersamonia dispar centralitaliae* Verity, 1943—115:61—Syntypes 4♂♂, 2♀♀ [italy]: Viareggio: Fosso Abate: VII [Verity leg.]; rest of the type-series destroyed by museum pests.

***citragordius** (ra)—*Heodes alciphron citragordius* Verity, 1943—115:45—Syntypes 17♂♂, 15♀♀ [Italy: Alpi Marittime]: Terme di Valdieri: [1375 m]: 8-29 VIII 1909, 3-16 VIII 1938, VIII [18]98: Verity [leg.].

**chryseis** (if)—*Lycaena escheri chryseis* Turati & Verity, 1911—015:258—Holotype ♀ [Italy: Alpi Marittime]: Valdieri: 15 VII [19]11: [Verity leg.].

***claracaelestis** (ra)—*Polyommatus icarus claracaelestis* Verity, 1949—116:146—Syntypes 4♂♂, 2♀♀ [France]: Charente-Infre [= Charente-Maritime]: Dompiere-sur-Mer: 2-3 VI 1911, 1 IX 1911, 16 VIII 1913, 29 VIII 1918.

**claracaerulea** (if)—*Cyaniris semiargus semiargus claracaerulea* Verity, 1943—115:237—Holotype ♂ [Italy]: Trentino: Groste: [2400-2900 m]: 25 VIII [1]926; Fiori [leg.].

**claraesimilis** (if)—*Philotes baton claraesimilis* Verity, 1943—115:119—Holotype ♂ [Italy]: Marche: Monti Sibillini: Bolognola: [1200 m]: 5 IX [1937]: Querci [leg.].

***claralpina** (ra)—*Lycaeides argus claralpina* Verity, 1931—081:53—Syntypes 8♂♂, 6♀♀ [Italy: Alpi Marittime]: Valdieri: [1375 m]: 17-31 VII [19]11: [Verity leg.].

***clarasiatica** (ra)—*Lycaeides argus clarasiatica* Verity, 1931—081:62—Syntypes 1♂, 1♀ [U.S.S.R.]: Gouv. Irkutsk: Sajan mont. or.: Mondy: Chulugaischa: 2600 m.

***claraobscura** (ra)—*Lycaeides argus claraobscura* Verity, 1931—081:54—Syntypes 5♂♂ [France]: Savoie: Bonneval s. Arc: Vallee Arc: 1800-2000 m: 11-25 VII

[19]27: Coll. Stempffer.

**clarior** (if)—*Agrodiaetus damon clarior* Verity, 1943—115:326—Syntypes 4♂♂, 7♀♀ Suisse: Neuchatel: Dombresson: VII 1917: Bolle [leg.]; [Giura]: St. Gergues: Nyon: 4 VIII [19]07.

**clorinda** (sf)—*Tarucus balcanicus clorinda* Verity, 1938—109:8—Syntypes 9♂♂, 5♀♀ [Greece]: Macedonia: Salonica [= Thessaloniki]: 1000 ft.: 12-29 V 1935: Querci [leg.].

**coeruleopunctata** (if)—*Chrysophanus hippothoe valderiana coeruleopunctata* Turati & Verity, 1911—015:244—Italy: Alpi Marittime: Valdieri.

**completa** (if)—*Glaucopsyche cyllarus pauper completa* Verity, 1919—042:29—Syntype ♂ [Italy: Toscana: Firenze]: Pian di Mugnone: 200 m: 2 VI 1915: [Querci leg.]; specimen remounted and relabelled.

**CORONA** (sp)—*Lysandra corona* Verity, 1936—098:106—Syntypes 2♂♂ [Iran]: Persia: S. Elburs: Kenderan: ca. 3000 m: 3-9 VII [1929]: Coll. Wagner, Wien—Probably a distinct species.

**correpta** (sf, ra)—*Agriades hylas correpta* Verity, 1920—042:144—Syntypes 10♂♂,7♀♀ Italia centrale: Marche: Piceno: Monti Sibillini, Massiccio Sibillini: Bolognola, Faggeti di Bolognola: 1200-1500 m: 20 VI-27 VII 1913, 5 IX 1913, 8 VII-24 VIII 1918, 10 VIII 1919: Querci [leg.].

***cretaephilonome** (ra)—*Lycaeides argus cretaephilonome* Verity, 1931—081:66—Syntypes 5♂♂, 1♀ [France]: Gironde: Soulac: 23 VII 1922, VIII 1928: Coll. Cassay; all labels poorly legible, some with incomplete data.

***cuencana** (ra)—*Agriades albicans cuencana* Verity, 1927—065:208—Syntypes 2♂♂ Espana: Nueva Castille: Cuenca: Valdemoro: 7 VII [1]920: Fernandez [leg.].

***dealbata** (ra)—*Latiorina glandon dealbata* Verity, 1926—058:105—Syntype 1♂ [Italy]: Südtirol: [Ortler]: Giocgo dello Stelvio: 2500 m: 191[?]: Wagner [leg.]—Beuret (1961): *Agriades glandon dealbata* [nec Verity], subspecies.

***demissa** (ra)—*Leosopis roboris demissa* Verity, 1943—115:342—Syntypes 1♂, 2♀♀ [France]: Var: Sainte-Baume: [700 m]: 15 VI 1914; Pyrenees-[Orientales]; A[lpi]M[arittime]: 16 VI [19]24: Coll. Stempffer—Manley & Allcard (1970): *Leosopis roboris demissa* [nec Verity], subspecies.

**detersa** (if)—*Lycaena bellargus detersa*, Verity 1911—016:276—Italy: Costa Toscana: Forte dei Marmi.

**dilutior** (sf)—*Everes alcetas dilutior*, Verity 194—094:34—Italy: Firenze.

**diminuta** (sf)—*Everes alcetas diminuta* Verity, 1919—042:47—Syntype(?) ♀ Italia centrale: Toscana: Firenze: Fosso Vignone: 8 V 1919: Querci [leg.].

***diniae** (ra)—*Agriades coridon diniae* Verity, 1926—058:124—Syntypes 8♂♂, 2♀♀ [France: Provence]: Vaucluse: Mont Ventoux: 15 VIII 1911: Ackaray [leg.]; Bass[es]-Alp[es]: Digne.

**enervis** (ra)—*Agriades hylas enervis* Verity, 1926—058:122—Syntypes 3♂♂ Austria inf.: [Wien]: Klosterneub[ur]g: Buchberg: 20-28 V 1920: Hofer [leg.]—Verity considered *Papilio dorylas* Denis & Schiffermuller, 1775 nomen nudum and named this race instead of validating it; his action was unjustified.

**etrusca** (ra, sf)—*Agriades thetis etrusca* Verity, 1919—042:29—Syntypes 9♂♂, 15♀♀ Italy: Toscana: Firenze: Pian di Mugnone: 200 m: 8-17 VIII 1916: Querci leg.;

all specimens remounted and relabelled.

***exuberans** (ra)—*Hirsutina admetus exuberans* Verity, 1926—058:121—Syntypes 4♂♂, 1♀ [Italy: Piemonte]: Alpi Cozie: Val Susa: Oulx [= Ulzio]: 1100 m: 25 VII-5 VIII 1925: Verity [leg.].

***ferenigra** (nn)—*Aricia nicias ferenigra* Verity, 1943—115:216—Replacement name for unavailable infrasubspecific name [*Lycaena*] *donzelii on obscura* Courvoisier, 1910 said to be preoccupied by *Lycaena arion obscura* Christ, 1878—Beuret (1961): *Aricia nicias frenigra* [nec Verity], subspecies.

***fiorii** (ra)—*Strymon ilicis fiorii* Verity, 1943—115:358—Syntypes 1♂, 2♀♀ [Italy]: Emilia: [Ferrara]: Mesola: 13 VI [1]934: Fiori [leg.].

**florentina** (ra)—*Lycaena aragonensis rezniceki florentina* Verity, 1916—032:517—Syntypes 4♂♂, 6♀♀ [Italy: Toscana]: Firenze: Pian di Mugnone: [200 m]: 24 V [19]29, 30 V [19]31, 10 VI [19]29, 9-25 VI [19]31, 17 VI [19]37: Verity [leg.].

***frigidior** (ra)—*Strymon acaciae frigidior* Verity, 1926—058:125—Syntypes 2♂♂, 5♀♀ [N. Italy: Torino]: Alpi Cozie: Oulx [= Ulzio]: Val Susa: 110 m: 4-21 VII [19]25: Verity [leg.].

***fumosa** (ra)—*Agriades coridon fumosa* Verity, 1926—058:123—Syntypes 7♂♂, 2♀♀ [France]: Oise: Moreuil: Plateau St. Claude: 1-13 VIII 1919.

**fuscensthetis** (sf)—*Lysandra bellargus fuscens fuscensthetis* Verity, 1943—115:297.

***galliae** (ra)—*Agriades coridon galliae* Verity, 1926—058:123—Syntypes 5♂♂, 8♀♀ [France: Paris]: Seine-et-Oise: Lardy: 13 VIII 1916.

***galliaealbicans** (ra)—*Lysandra albicans galliaealbicans* Verity, 1939—112:213—Syntypes 12♂♂, 4♀♀ [France]: Aude: Carcassone: 25 VII [19]29; Var: Nines: [illegible]: 27 VII [19]26: Gaillard [leg.].

***germanella** (ra)—*Agriades coridon germanella* Verity, 1926—058:125—Syntypes 7♂♂, 6♀♀ [Germany]: Bavaria: Regensburg: Velburg: 8 VIII [19]13, 13 VII [19]23, VII [19]18: Metschl [leg.].

***glaciata** (ra)—*Aricia chiron glaciata* Verity, 1921—042:174—Syntypes 2♂♂ [Italy: Südtirol]: Ortler: 1800 m: 3-10 VIII 1920: Verity [leg.].

***glaucargester** (ra)—*Lysandra argester glaucargester* Verity, 1939—112:222—Syntype 1♂ [Italy]: Abruzzi: Gran Sasso: 1300-1500 m: 28 VII 1939: Romei [leg.].

***gravesi** (ra)—*Heodes virgaureae gravesi* Verity, 1929—070:129—Syntypes 3♂♂, 3♀♀ [France]: Lozere: Gonecoules: Malmontet: 1200 m: 14 VII [19]24, 11 VII [19]26, 14-19 VIII [19]28: Gaillard [leg.]; data on labels poorly legible, some incomplete.

***gravesica** (ra)—*Heodes virgaureae gravesica* Verity, 1929—070:129—Syntypes 6♂♂, 12♀♀ [France: Cevennes]: Mt. Aigoual: 15-19 VIII 1928: Gaillard [leg.].

**hemialpium** (if, sr)—*Meleageria daphnis alpium hemialpium* Verity, 1943—115:332—Syntypes 6♂♂, 2♀♀ [Italy: Torino: Alpi Cozie]: Meana di Susa: 600-1000 m: 21-24 VII [19]41: Pomeli [leg.].

***hibera** (ra)—*Lysandra coridon hibera* Verity, 1939—112:215—Syntypes 2♂♂, 1♀ [Spain]: Aragon: [Teruel: Albarracin]: Tramacastilla: 1300 m: 28-29 VII 1924: Querci [leg.].

**hibernata** (sf, ra)—*Agriades thersites hibernata* Verity, 1919—042:44—Italy: Alpi Cozie: Sestrieres, Orsiere.

***hispanafusca** (ra)—*Lycaeides argus hispanafusca* Verity, 1931—081:43—Syntypes 9♂♂, 3♀♀ Espana: Nueva Castille: Cuenca: Fernandez [leg.]—Manley & Allcard (1970): *Plebejus argus hispanafusca* [nec Verity], subspecies.

***hispanagallica** (ra)—*Agriades coridon hispanagallica* Verity, 1926—058:125—Syntypes 5♂♂ [France]: Ariege: Belesta: 10-11 IX 1909: Powell [leg.].

***hypochionalpina** (ra)—*Lycaeides argus hypochionalpina* Verity, 1931—081:52—Syntypes 4♂♂, 1♀ [France]: Basses-Alpes: Annot: 700 m: 8-13 VII [19]26: Coll. Stempffer.

***inalpina** (ra)—*Thecla ilicis inalpina* Verity, 1911—016:272—Syntypes 4♂♂, 3♀♀ [Switzerland]: Vallese: Wulfschlegel [leg.].

***inalpina** (ra)—*Agriades thetis inalpina* Verity, 1919—042:29—Syntypes 2♂♂, 1♀ [Switzerland]: Vallese: Wulfschlegel [leg.].

***inalpinus** (ra)—*Chrysophanus virgaureae inalpinus* Verity, 1913—023:187—Syntypes 6♂♂, 13♀♀ Italy: Alpi Marittime: Valdieri: 1400 m: VII-VIII 1909: Verity leg.; all specimens remounted and relabelled.

***inanis** (ra)—*Aricia anteros inanis* Verity, 1938—109:5—Syntypes 9♂♂, 12♀♀ [Greece]: Macedonia: Olympus: [Stavros: 700 m]: 15 VI-18 VII 1935: [Romei leg.]—Name proposed for ecological form.

**infracacaotica** (if)—*Aricia medon infracacaotica* Verity, 1920—042:149.

**infracana** (sf)—*Thersamonia thersamon thersamon infracana* Verity, 1943—115:64—Syntypes 18♂♂, 7♀♀ [Italy]: Lazio: Roma: [Verano]: 100 m: 24-29 IX 1939: Romei [leg.].

**infracanaomphale** (nomen nudum)—*Thersamonia thersamon thersamon infracanaomphale* Verity, 1943—115:64—Name proposed hyphenated and attributed to 'Vrty.-Esp.', published without description, definiton or indication.

***infracandida** (ra)—*Aricia medon infracandida* Verity, 1920—042:148—Holotype ♂ Syria [= Lebanon]: [Beyrouth]; type: *infracandida.*

**infralbens** (if)—*Aricia medon infralbens* Verity, 1920—042:148.

**infralunulata** (if)—*Agrodiaetus dolus infralunulata* Verity, 1943—115:323—Italy: Abruzzi: Gran Sasso.

**infrapallida** (if)—*Lycaena phaeas infrapallida* Verity, 1943—115:52—Italy: Sicily: Palermo: Monreale: San Martino: 800 m.

**infrapallida** (if)—*Syntarucus pirithous infrapallida* Verity, 1943—115:80—Holotype ♂ [Italy: Toscana: Lucca]: Forte d[ei] M[armi]: 28 VI [19]23: [Verity leg.]; 'olotipo': *infrapallida.*

**infraplumbea** (sf)—*Aricia medon infraplumbea* Verity, 1920—042:149.

***inornata** (ra)—*Thecla ilicis inornata* Verity, 1911—016:272—Syntype ♂ [Italy: Toscana]: Firenze: 2 VII [????]: [Verity leg.].

***insulana** (ra)—*Agriades coridon insulana* Verity, 1926—058:123—Syntypes 15♂♂, 2♀♀ [England]: Kent: Sevenoaks: 24 VIII 1879: Conquest [leg.].

**interjecta** (sf)—*Agriades thersites interjecta* Verity, 1919—042:44—Syntype ♀ Italy: Firenze: Pian di Mugnone: 21 VI 1915: Querci leg.; specimen remounted and relabelled.

***interjecta** (ra)—*Bithys quercus interjecta* Verity, 1919—042:48—Syntypes 1♂, 2♀♀ Italia centrale: Toscana: Colline di Firenze: 400 m: 18 VII-12 VIII 1914: Querci [leg.].

**italaegiades** (sf)—*Plebejus argus aegiades italaegiades* Verity, 1943—115:197—Syntypes 20♂♂, 3♀♀ [Italy: Torino]: Casalborgone: 10-29 VIII [1]914: [Rocci leg.].

***italagallica** (ra)—*Agriades coridon italagallica* Verity, 1926—058:124—Syntypes 11♂♂, 1♀ [Italy: Piemonte]: Alpi Cozie: Torino: Cesana: 1300 m: 15-24 VII 1925; Clavieres: 1800 m: 29 VII 1925; [all] Verity [leg.].

***italaglauca** (ra)—*Lysandra syriaca italaglauca* Verity, 1939—112:220—Syntypes 6♂♂ [Italy]: Abruzzi: Gran Sasso: 1300-1400 m: 3-8 VII 1939: Romei [leg.].

**italanigrans** (sr)—*Plebejus argus italorum italanigrans* Verity, 1943—115:191—Syntypes 7♂♂, 6♀♀ [Italy]: Abruzzi: Gran Sasso: 1300-1700 m: 1 VII-30 VIII 1939: Romei [leg.].

***italapulchra** (ra)—*Lycaeides idas italapulchra* Verity, 1943—115:169—Syntypes 6♂♂, 7♀♀ [Italy]: Abruzzi: Gran Sasso: 1300-1500 m: 22 VII-15 VIII 1939: Romei [leg.]; Lazio: Monte Meta: Colle Alto: 1200 m: 8 VIII [19]40.

**italaveris** (sf)—*Loweia dorilis italorum italaveris* Verity, 1924—053:108—Syntypes 3♂♂, 1♀ Italia centrale: Toscana: [Firenze]: Pian di Mugnone: 200 m: 23 IV 1918, 4 V 1916: Querci [leg.].

***italica** (ra)—*Thecla acaciae italica* Verity, 1919—042:48—Syntypes 8♂♂, 10♀♀ Italia centrale: Toscana: Colline di Firenze: 400 m: 1 VII-12 VIII 1914, 12 VII 1918: Querci [leg.].

**italiae** (sf)—*Thersamonia dispar cetralitaliae italiae* Verity, 1943—115:61—Italy: Viareggio: Fosso Abate.

***italorum** (ra)—*Loweia dorilis italorum* Verity, 1919—042:29—Syntypes 24♂♂, 5♀♀ Italia centrale: Lucca: Fiume Camaione: 300 m: 9 VIII-10 IX 1915: Querci [leg.].

***italorum** (ra)—*Plebeius argus italorum* Verity, 1919—042:45—Syntypes 6♂♂, 6♀♀ [Italy: Toscana: Appennino Pistoiese]: Abetone: [1300 m]: 7 VII [19]12: [Verity leg.].

***jurae** (ra)—*Agriades coridon jurae* Verity, 1926—058:123—Syntypes 40♂♂, 12♀♀ Suisse: [Jura]: Neuchatel: Dombresson: 17-28 VIII 1917, VIII 1918: Bolle [leg.].

**LARIA** (nn)—*Lycaeides argyrognomon laria* Verity, 1937—106:38—Replacement name for *Lycaena argus ligurica* Oberthür, 1910, said to be preoccupied by *Lycaena arion ligurica* Wagner, 1904.

**lateacaerulea** (if)—*Cupido minimus lateacaerulea* Verity, 1943—115:97—Holotype ♂ [Italy]: Abruzzi: Gran Sasso: 1300-1700 m: 4 VII 1939: Romei [leg.]; 'olotipo': *lateacaerulea.*

**latolimbo** (if, ra)—*Plebeius idas latolimbo* Verity, 1927—063:7—Syntypes 2♂♂ [Yugoslavia]: Carniolia: Pokojisce: 1 VII 1925: Hafner [leg.].

**lunensis** (if, ra)—*Plebeius argus lunensis* Verity, 1919—042:45—Syntypes 3♂♂, 2♀♀ [Italy]: Spezia: Petrusola: 14 VIII 1913: Verity leg.; all specimens remounted and relabelled.

**luteumfera** (if)—*Everes alcetas luteumfera* Verity, 1919—042:47—Syntypes 1♀ [Yugoslavia]: Istria: Portorosa: 5 IX [19]26: Verity [leg.].

***macedonica** (ra)—*Aricia montensis macedonica* Verity, 1936—101:7—Syntypes

9♂♂, 1♀ [Greece]: Macedonia: Olympus: 2500-4500 ft.: 15 VI-4 IX 1935: Romei [leg.].

***macra** (ra)—*Polyommatus meleager macra* Verity, 1920—042:144—Syntypes 4♂♂,3♀♀ Italia centrale: [Toscana]: Lucca: Prato Fiorito: 1000 m: 27 VII-6 VIII 1915: Querci [leg.].

**macraalpiumclara** (nomen nudum)—*Polyommatus meleager macraalpiumclara* Verity, 1936—101:7—Name for race published hyphenated without description, definition or indication.

***macromargarita** (ra)—*Agriades hylas macromargarita* Verity, 1926—058:121—Syntypes 14♂♂, 1♀ [Italy: Alpi Marittime]: Valdieri: [1375 m]: VII-VIII [18]98, 23 VII-1 VIII [19]09, 1 VIII [19]11: [Verity leg.].

***macromelanica** (ra)—*Maculinea teleius macromelanica* Verity, 1943—115:147—Syntypes 1♂, 2♀♀ [Italy: Torino]: Torre Pollice: [500 m]: 22 VII [19??].

***madriti** (ra)—*Turania hylas madriti* Verity, 1928—066:143—Syntypes 2♂♂, 1♀ [Spain: Madrid]: Escorial: 10 V [19]12—Manley & Allcard (1970): *Philotes baton madriti* [nec Verity], subspecies.

**magnaglandon** (nn)—*Agriades glandon magnaglandon* Verity, 1949—116:134—Replacement name for *Lycaena orbitulus oberthueri* Staudinger, 1901, which is said to be primary junior homonym of *Lycaena elvira oberthueri* Grumm-Grshimailo, 1887, apparently of infrasubspecific rank (subvarietas).

***magnagraeca** (ra)—*Plebeius argus magnagraeca* Verity, 1936—101:6—Greece: Olympus: 300 m: V—Higgins (1976): *Lycaeides idas magnagraeca* [nec Verity], subspecies.

***magnalpina** (ra)—*Plebeius idas magnalpina* Verity, 1927—063:10—Syntypes 10♂♂, 4♀♀ [Italy: Torino]: Alpi Cozie: Cesana: 1300 m: 11 VII-1 VIII 1925: Verity [leg.].

***magnalutea** (ra)—*Lysandra bellargus magnalutea* Verity, 1943—115:296—Syntypes 9♂♂, 5♀♀ [Italy]: Torino: Casselette: pendici S. Musine: 450 m: 5 VI 1937, 12 V 1940; Torino: Venaria: Testura: 25 VI 1937; Lago di Maggiore: Intra: S. Bernardino: 200 m, Piano Quaggie: 950 m: 20-27 VII 1934, 12 V 1934; [all] Rocca, Verity [leg.].

**magnaluteabellargus** (sr)—*Lysandra bellargus magnalutea magnaluteabellargus* Verity, 1943—115:297—[N. Italy]: Vanzone: Anzasca: 700 m—Originally published hyphenated, the authorship attributed to Rottemburg & Verity.

**magnapunctifera** (ra)—*Lysandra bellargus punctifera magnapunctifera* Verity, 1937—108:5—Syntype 1♂ Morocco: [Middle Atlas Mts.]: Ifrane: 1 X 1933: Wikely [leg.].

**maja** (sf)—*Agriades thetis etrusca maja* Verity, 1919—042:29—Syntypes 12♂♂, 11♀♀ Italy: Toscana: Firenze: Pian di Mugnone: 200 m: 16-30 V 1915: Querci [leg.]; all specimens remounted and relabelled.

**major** (if)—*Meleageria daphnis major* Verity, 1943—115:332.

**majuspunctata** (ra, if)—*Cupido sebrus majuspunctata* Verity, 1934—094:34—Syntypes 15♂♂, 10♀♀ [Turkey]: Asia Minor c.: Ak-Chehir: 16 V-15 VII [????]: Coll. Wagner, Wien.

**maritimalpium** (nn)—*Glaucopsyche cyllarus maritimalpium* Verity, 1928—066:

141—Replacement name for (apparently unavailable infrasubspecific name) *Lycaena alexis alpina* Turati & Verity, 1911 which is said to be a primary junior homonym of (apparently available species-group name) *Lycaena idas alpina* Berce, 1867.

***maritimarum** (ra)—*Lysandra coridon maritimarum* Verity, 1943—115:312—Syntypes 8♂♂, 8♀♀ [Italy: Alpi Marittime]: Valdieri: [1375 m]: 20 VIII [19]09, 25 VII [19]09, 18 VII-20 VIII [19]11, 3-16 VIII [19]38: Verity [leg.].

***media** (ra)—*Vacciniina optilete media* Verity, 1943—115:242—Syntypes 2♂♂, 1♀ [N. Italy]: Alpi Carniche: Sappada: 1300 m: 19 VII [19]26; S. Stefano di Cadore: 900 m: 16 VII [19]26; [all] Verity [leg.]; Alpi Venoste: S. Valentino: Malga della Chiesa: 2000 m: 29 VII 1939: Rocca [leg.].

***mediomontana** (ra)—*Heodes virgaureae mediomontana* Verity, 1929—070:131—Syntypes(?) 6♂♂, 1♀ [Italy]: Torino: Alpi Cozie: Cesana: 15 VII [1]925: Verity [leg.]; status of type-series uncertain—Same name used by Verity also for 'synexerge'—Beuret (1953): *Heodes virgaureae mediomontana* [nec Verity], subspecies.

***melanopostmater** (ra)—*Glaucopsyche cyllarus melanopostmater* Verity, 1928—066:141—Syntypes 4♂♂, 1♀ [Algeria]: Oran: Aflou: coll. Deckert—Higgins & Riley (1970): *Glaucopsyche alexis melanoposmater* [nec Verity], subspecies.

**meridiana** (ra, sf)—*Agriades thersites meridiana* Verity, 1919—042:43—Syntypes 18♂♂, 9♀♀ Italy: Toscana: Firenze: Pian di Mugnone: 200 m: 22 IV-21 VI 1915: Querci leg.; all specimens remounted and relabelled.

***meridioccasus** (ra)—*Agrodiaetus damon meridioccasus* Verity, 1951—116:176—Syntypes 2♂♂ [France]: Lozere: Causse Mejean: 8 VIII [19]26: [Stempffer leg.].

***micreros** (ra)—*Polyommatus eros micreros* Verity, 1949—116:148—France: Pyrenees: Vernet-les-Bains: Col Vert.

***microchroa** (ra)—*Maculinea arion microchroa* Verity, 1948—116:106—Syntypes 3♂♂ [France]: Siene-et-Oise; [Paris]: Lardy; Angouleme: Voenil: 4 IX [19]24.

***microhypochiona** (ra)—*Lycaeides argus microhypochiona* Verity, 1931—081:38—Syntypes 7♂♂, 13♀♀ [Spain]: Aragon: [Teruel]: Albarracin: 1100 m: 4-24 VI 1924: Querci [leg.]—Manley & Allcard (1970): *Plebejus argus microhypochiona* [nec Verity], subspecies.

***micromargarita** (ra)—*Agriades hylas micromargarita* Verity, 1926—058:121—Syntypes 6♂♂, 1♀ [N. Italy: Torino]: Alpi Cozie: Val Susa: Oulx [= Ulzio]: 1100 m: 4-23 VII [19]25; Cesana: 1300 m: 11-24 VII [19]25; [all] Verity [leg.].

**micromelanica** (ra, sr)—*Maculinea teleius micromelanica* Verity, 1943—115:147—Syntypes 7♂♂ [Switzerland]: Ginevra [= Geneve]; original rank uncertain: called 'variazione locale' and treated as race or below race—Beuret (1957): *Maculinea teleius micromelanica* [nec Verity], subspecies.

**micrometioche** (sf)—*Scolitantides orion metioche micrometioche* Verity, 1943—115:112—Syntypes 2♂♂, 3♀♀ [N. Italy]: Lago Maggiore: Intra: 28 IV-4 V [19]27: [Verity leg].

***micrometioche** (ra)—*Scolitantides orion micrometioche* Verity, 1943—115:112—Syntypes 1♂, 1♀ [N. Italy]: Alpi Carniche: Sappada: 1300 m: 16 VII 1926: Verity [leg.]; Forni Avoltri: 7 VIII [18]96: Rocci [leg.].

**microrientalis** (sf)—*Lysandra thersites microrientalis* Verity, 1935—096:244—[Turkey: Malatya]: Tecde.

***microsephyrus** (ra)—*Plebeius sephyrus microsephyrus* Verity, 1935—096:245—Syntpes 2♂♂ [Turkey]: Asia Minor: Malatya: Tecde: 27 V [????].

***microsticta** (ra)—*Agriades escheri microsticta* Verity, 1929—071:158—Syntypes 6♂♂, 7♀♀ [N. Italy: Torino]: Alpi Cozie: Cesana: 1300 m: 11 VII-1 VIII 1925: Verity [leg.].

**minor** (if)—*Cupido minimus minor* Verity, 1943—115:99.

**minor** (if)—*Meleageria daphnis minor* Verity, 1943—115:332.

**minor** (if)—*Lysandra albicans florentina minor* Verity, 1943—115:306—Syntypes 1♂, 2♀♀ [Italy: Toscana]: Firenze: Pian di Mugnone: 29 VIII, 6 IX, 13 IX [19]35: Verity [leg.].

**minorata** (if)—*Aricia anteros minorata* Verity, 1938—109:5—Syntypes 11♂♂ [Greece]: Macedonia: Olympus: [S. Dionisio: 800 m]: 1-12 VI 1936, 17 VI-20 VII 1935: Romei [leg.].

**minoratissima** (sf)—*Aricia anteros minoratissima* Verity, 1938—109:6—Syntypes 43♂♂, 13♀♀ [Greece]: Macedonia: Olympus: [S. Dionisio: 800 m]: 20 VII-3 IX 1936: Romei [leg.].

**minusornata** (sf)—*Aricia cramera aridogenita minusornata* Verity, 1928—067:182—Syntypes 15♂♂, 2♀♀ Portugal: Alemtejo: 10 m: 16-23 IV 1927: Querci [leg.].

***minuta** (ra)—*Thecla spini minuta* Verity, 1919—042:48—Syntypes 2♂♂, 1♀ Italia centrale: [Marche]: Piceno: Massiccio Sibillini: Bolognola: 1200 m: 18-23 VII 1918: Querci [leg.].

***minutepunctata** (ra)—*Agriades coridon minutepunctata* Verity, 1926—058:124—Syntypes 2♂♂ [France]: Hte. Garonne: Luchon: 1-3 VIII 1910: Ackaray [leg.].

***minutepunctata** (ra)—*Heodes alciphron minutepunctata* Verity, 1948—116:62—France: Nimes: Pont-Saint-Esprit: La Valbonne.

***mira** (ra)—*Lycaena idas mira* Verity, 1915—028:230—Syntypes 12♂♂, 11♀♀ Italia centrale: Toscana: Colline di Firenze: [Monte Conca]: 400 m: 24 VI-5 VII 1914: Querci [leg.]; all specimens remounted and relabelled.

***mirabilis** (ra)—*Loweia alciphron mirabilis* Verity, 1919—042:28—Syntypes 6♂♂, 4♀♀ [Italy: Toscana]: Firenze: Monte Senario: [700 m]: 5 VI [19]08, 17 VI [19]04, 1 VII [1]903: 12 VII 1918: Verity, Querci [leg.].

***mirus** (ra)—*Chrysophanus hippothoe mirus* Verity, 1913—023:188—Syntypes 1♂, 1♀ [France]: Pyrenei: [Gedre].

**misera** (if, sf)—*Plebeius idas misera* Verity, 1919—042:46—Holotype ♂ [Italy: Toscana]: Firenze: X [19]08: [Verity leg.]; type: *misera*.

**mixta** (if)—*Lycaenopsis argiolus mixta* Verity, 1919—042:45—Holotype ♀ [England: Lodon]: Woodford: Epping Forest: 7 V 1876: Conquest [leg.].

***mixtalpina** (ra)—*Heodes tityrus mixtalpina* Verity, 1948—116:60—Syntypes 2♂♂ [France]: Alpes-Maritimes: Environs du Boreon: Lac du Tre Colpes: 2200 m: 25 VII [19]35; Piera Emeccia: 1800 m: 18 VII 1934; [all] Gazell [leg.].

***modica** (ra)—*Plebeius sephyrus modica* Verity, 1935—096:245—Syntypes 25♂♂, 2♀♀ [Turkey]: Asia Minor c.: Ak-Chehir: 16 V-15 VI [????]: Coll. Wagner, Wien.

**modicior** (sf, ra)—*Aricia anteros modicior* Verity, 1938—109:5—Syntypes 9♂♂ [Greece]: Macedonia: Olympus: [Prionia: 1500 m]: 23 V-3 VI 1936: Romei [leg.].

***montanabella** (ra)—*Aricia medon montanabella* Verity, 1928—067:180—Syntypes 23♂♂, 13♀♀ [Spain]: Nueva Castilla: Cuenca: Huelamo: 1200 m: 6 VIII-8 IX 1926; Villacarbas: 1200 m: 13 VII-8 IX 1926; Querci [leg.]—Manley & Allcard: *Aricia montensis montanabella* [nec Verity], subspecies.

**montanaclara** (if, ra, sr)—*Cyaniris semiargus montana montanaclara* Verity, 1943—115:239—Syntypes 9♂♂, 1♀ [Italy]: Alpi Cozie: Sestrieres: 2035 m: 8 VIII 1925; Clavieres: 1800 m: 29 VII 1925; [all] Verity [leg.].

**MONTENSIS** (nn)—*Aricia medon montensis* Verity, 1928—067:180—Replacement name for *Lycaena astrarche montana* Heyne, 1895, preoccupied by *Lycaena acis montana* Meyer-Dürr, 1852, and for its junior subjective synonym *Lycaena agestis nevadensis* Oberthür, 1910, said to be primary junior homonym of *Lycaena argus nevadensis* Oberthür, 1896; questions regarding the nomenclature of the butterfly usually referred to as *Aricia montensis* are more difficult than appreciated by all past authors and urgently require a full taxonomic treatment of the whole complex of taxa involved, which is beyond the scope of this paper. Subjectively on taxonomic grounds *montensis* may be considered conspecific with *Aricia allous* Geyer, 1837 as its junior subjective synonym.

***montiummagna** (ra)—*Aricia medon montiummagna* Verity, 1928—067:181—Syntypes 4♂♂, 3♀♀ Italia centrale: Toscana: Alpi Apuane: [Monte] Sombra: 1200-1400 m: 18-21 VI 1920: Querci [leg.].

**montiummagnaagestis** (ra, tf)—*Aricia agestis montiummagnaagestis* Verity, 1949—116:130—Syntypes 6♂♂ [France]: Cevennes: Causse du Larzac: Hospitalet: 800 m: 8 VII 1928: Gaillard [leg.].

***narbonensis** (ra)—*Agriades coridon narbonensis* Verity, 1926—058:123—Syntypes 4♂♂, 5♀♀ [France]: Provence: [Bouches-du-Rhone]: 3-8 VIII 1924: Foulquier [leg.]; Var: St. Zacharie: 8 VIII [19]26.

**nigrescens** (nn)—*Lysandra coridon nigrescens* Verity, 1943—115:309—Replacement name for infrasubspecific unavailable name *Agriades coridon atrescens* Verity, 1926, said to be preoccupied by another unavailable infrasubspecific name *Agriades coridon atrescens* Tutt, 1910.

**nigrioeleus** (nomen nudum)—*Rumicia phlaeas nigrioeleus* Verity, 1920—042:5—Name for a 'grade' of variation or transitional form published without description, definition or indication.

**nigrovelata** (if)—*Cyaniris semiargus semimontana nigrovelata* Verity, 1943—115:238—Syntypes 1♂, 1♀ [Italy: Trento]: Dol[omiti] occ.: Val di Gares: Ponte di Ferrade: 1037 m: 21-22 VIII 1937: Rocca [leg.].

**obliterata** (if)—*Chrysophanus hippothoe valderiana obliterata* Turati & Verity, 1911—015:244—Holotype(?) ♂ [Italy/Switzerland]: Simplon: VII 1904; type: *obliterata*.

**obscurata** (sf)—*Scolitantides baton obscurata* Verity, 1919—042:29—Type-material probably destroyed by museum pests.

***oceanitis** (ra)—*Heodes tityrus oceanitis* Verity, 1948—116:58—Syntypes 40♂♂, 13♀♀ France: Vendee: Puybelliard: 21-28 V 1917: Querci [leg.]; [Gironde]: Marsac: P. Cavignac: Bernee: 20 V [19]25; part of type-series with group label, without data labels under individual specimens.

**october** (sf)—*Lysandra bellargus etrusca october* Verity, 1943—115:294—Italy: Firenze: Pian di Mugnone.

***olympena** (ra)—*Lysandra escheri olympena* Verity, 1936—101:8—Syntypes 21♂♂, 12♀♀ [Greece]: Macedonia: Olympus: 2500 ft.: 14 VI-8 VIII 1935: Romei [leg.].

***opisthochros** (ra)—*Paleoloweia tityrus opisthochros* Verity, 1939—111:186—Syntypes 4♂♂, 1♀ Iran: Elbursgebirge: Nissa: 20-27 VII 1936: Brandt leg.

***opulenta** (ra)—*Plebeius idas opulenta* Verity, 1927—063:7—Syntypes 9♂♂, 5♀♀ [N. Italy]: Lago Maggiore: Intra: Pian Quaggie: 950 m: 15-23 VI 1922: Querci [leg.]—Beuret (1961): *Lycaeides idas opulenta* [nec Verity], subspecies.

***orientaloides** (ra)—*Lycaeides argus orientaloides* Verity, 1931—081:48—N. Iran.

***pallidecolor** (ra)—*Meleageria daphnis pallidecolor* Verity, 1943—115:333—Syntypes 2♂♂ [Italy]: Sicilia: Madonie: 1914: Coll. Ragusa.

**pallidecanariensis** (if)—*Aricia cramera pallidecanariensis* Verity, 1928—067: 182—N. Africa—Name proposed conditionally for variation not known to exist.

**pallidecramera** (if)—*Aricia cramera pallidecramera* Verity, 1928—067:182—N. Africa—Name proposed conditionally for variation not known to exist.

**pallidefulva** (sf, ra)—*Aricia medon pallidefulva* Verity, 1920—042:149—Syntypes 4♂♂, 2♀♀ Italia centrale: Toscana: Firenze: Pian di Mugnone: 200 m: 6 VIII, 6-12 IX 1917: Querci [leg.].

***pallidepicta** (ra)—*Palaeoloweia tityrus pallidepicta* Verity, 1934—094:16—Syntype 1♂ [France]: Vaucluse: Mont Ventoux: 15 VII 1911: Ackeray [leg.].

***pallidula** (ra)—*Plebeius argus pallidula* Verity, 1924—053:110—Syntypes 10♂♂, 9♀♀ Italia centrale: Piceno: Ascoli: Pizzo Tre Vescovi: 1700 m: 18-24 VII 1923: Querci [leg.].

**parabellargus** (if, hy)—*Lysandra albicans parabellargus* Verity, 1939—112:214—Syntype 1♂ [Turkey]: Asia Minor: Yozgat: 5000 ft.: VI-VII 1918: Capt. W. W. Phillips [leg.]: 1919-22; probably described from a single specimen—Original rank uncertain: '[individual] form' or hybrid by implication.

***paraurydice** (ra)—*Palaeochrysophanus hippothoe paraeurydice* Verity, 1943—115:69—Syntypes 1♂, 1♀ [France]: Paris: F. Compiegne: 17 VI 1934.

**parallela** (if)—*Heodes alciphron parallela* Verity, 1943—115:42.

**PARAMELEAGER** (sp)—*Polyommatus parameleager* Verity, 1936—099:130—Syntype 1♂ Iran: Elbursgebirge: Tschalus-Mazanderan Strasse: Nordhang: ca. 1000 m: 22 VIII 1936: coll. Brandt.

***paraustera** (ra)—*Plebejus argus paraustera* Verity, 1943—115:199—Syntypes 4♂♂, 2♀♀ [N. Italy]: Alpi Pennine: Macugnaga: 1300 m: 18-24 VII [19]28: Verity [leg.].

**paravirgilia** (sr)—*Agrodiaetus dolus virgilia paravirgilia* Verity, 1943—115:325—Syntypes 1♂, 1♀ Italia merid.: Penins. Sorrentina: M. Faito: 800 m: VII 1920: Stauder leg.

**parvalaria** (if, sf)—*Lycaeides argyrognomon parvalaria* Verity, 1943—115:181—Syntypes 1♂, 3♀♀ [Italy]: Milano: Soria: 28 VII [19]29, Turbigo: 27 VII [19]30, Lago Maggiore: Taino: 2 IX [1]932: Rocci, Taccani [leg.].

***parvandereggi** (ra)—*Glaucopsyche cyllarus parvandereggi* Verity, 1938—109:4—Syntypes 4♂♂, 6♀♀ [Greece]: Macedonia: Salonika [= Thessaloniki]: 1000 ft.: 28

IV-18 V 1935, 26 IV 1937: Romei [leg.].

***parvaplumbea** (ra)—*Lysandra argester parvaplumbea* Verity, 1934—094:28—Syntypes 3♂♂, 1♀ [Switzerland: Wallis]: Martigny: 10-19 VIII 1932: Verity [leg.].

***pauper** (ra)—*Glaucopsyche cyllarus pauper* Verity, 1919—042:29—Italy: Firenze.

***peninsulae** (ra)—*Lycaena euphemus peninsulae* Verity, 1923—052:7—Syntypes 1♀ Italia centrale: Massacci di Bolognola: 1200 m: 26 VI 1922: Querci [leg.]; probably described from a single specimen.

***persaemagna** (ra)—*Lysandra bellargus persaemagna* Verity, 1937—108:3—Syntypes 3♂♂, 1♀ Iran: [Teheran]: Elbursgebirge: Keredj: 1200-1400 m: 2-16 V 1936: Brandt [leg.].

**petri** (ab)—*Agriades coridon petri* Verity, 1920—042:140—Italy: Toscana: Firenze, Mt. Fanna.

**pigmentocarens** (if)—*Callophrys rubi pigmentocarens* Verity, 1926—058:125—Holotype ♀ [Italy]: Alpi Cozie: Oulx [= Ulzio]: Val Susa: 110 m: 3 VI [19]25: Verity [leg.].

**polyphemusovalisquamosa** (sr)—*Polyommatus icarus polyphemus polyphemusovalisquamosa* Verity, 1943—115:258—N. Italy: Alpi Cozie.

***porrecta** (ra)—*Cyaniris semiargus porrecta* Verity, 1919—042:45—Syntypes 10♂♂, 11♀♀ Italia centrale: Piceno: Monti Sibillini: 1200 m: 28 VI 1913; Faggeti di Bolognola: 1400-1500 m: 10-30 VI, 11 VIII 1913; Massiccio Sibillini: 1200-1600 m; [all] Querci [leg.].

**porrectausonidarum** (sr)—*Cyaniris semiargus porrecta porrectausonidarum* Verity, 1943—115:237—Syntypes 11♂♂, 4♀♀ [S. Italy]: Costiera Calabra: Cosenza: Catena: San Fili: 900 m: 19 V-23 VI 1920: Querci [leg.].

**postacis** (sf, if)—*Cyaniris semiargus acis postacis* Verity, 1943—115:235—Syntypes 2♂♂ [France]: A[alpes]-M[aritimes]: [1000 m]: 5 VII [19]33: Coll. Gazell.

**postapenninigena** (sf)—*Lysandra bellargus apenninigena postapenninigena* Verity, 1943—115:295—Syntypes 42♂♂, 11♀♀ Italia centrale: Piceno: Monti Sibillini: Bolognola: 1200 m: 5-10 IX 1913, VIII 1915, 15-28 VIII 1918, 8-22 IX 1919, 29 VIII-9 IX 1937: Querci, Verity [leg.].

**postargester** (sf)—*Lysandra argester argester postargester* Verity, 1934—094:28—Syntype 1♂ [Austria]: Wien-Umgeb[ung]; probably described from a single specimen.

**postaustera** (sf)—*Plebejus argus austera posaustera* Verity, 1943—115:199—Syntypes 3♂♂ [Italy]; Lago Maggiore: Bee: [600]: VIII [1]900.

**postcandalus** (sf)—*Polyommatus candalus postcandalus* Verity, 1937—108:7—Syntypes 3♂♂ [Turkey]: Asia Minor c.: Ak-Chehir: VIII [19]29: Coll. Wagner, Wien.

**postenervis** (sf)—*Lysandra argester enervis postenervis* Verity, 1934—094:29—Austria: Wien(?).

**posticelantenigra** (if)—*Syntarucus pirithous posticelantenigra* Verity, 1938—109:9—Holotype ♂ [Greece]: Macedonia: Olympus: 1500 [m]: 13 VI 1936: Romei [leg.].

**posticobasipunctata** (if)—*Agrodiaetus ripartii posticobasipunctata* Verity, 1943—115:321—Syntype 1♀ France: Alpes-Maritimes: [Nice]: St. Barnabe: 12 VIII [19]37: Verity [leg.].

**postmagnalutea** (sf)—*Lysandra bellargus magnalutea postmagnalutea* Verity, 1943—115:296—Syntypes 11♂♂, 8♀♀ [N. Italy]: Alpi Pennine: Vanzone: 700 m: 11 VIII [19]28; Lago Maggiore: Intra, Bee, Vignone: 7-26 VIII 1940, 2 IX 1940; [all] Verity [leg.].

**postmargarita** (sf)—*Lysandra argester micromargarita postmargarita* Verity, 1943—115:283—Syntypes 1♂, 1♀ [Italy]: Piemonte: Val Susa: 1 VIII 1907; Alessandria: Acqui: 10 VIII [19]12.

**postmicrorientalis** (sf)—*Lysandra thersites postmicrorientalis* Verity, 1935—096:244—Turkey: Malatya: Tecde.

**postoceanitis** (sf)—*Heodes tityrus oceanis postoceanitis* Verity, 1948—116:58—Syntypes 3♂♂ [France]: Gironde: St. Come: Bazas: VIII 1918; Marsac: 14 IX 1924: Sorin [leg.]; Vendee: 20 VIII 1918.

**postpulcherrima** (sf)—*Polyommatus icarus pulcherrima postpulcherrima* Verity, 1943—115:254—Syntypes 12♂♂, 12♀♀ [Italy]: Sicily: messina: Zapulla: 8 VI 1930, 3 VI [19]33, 22 VI [19]34; Palermo: Mezzojuso: [550 m]: 29 VI [19]30, Cdaccia: VII, VI 1930.

**postpunctifera** (sf)—*Lysandra bellargus punctifera postpunctifera* Verity, 1937—108:5—Syntype ♂ [Morocco]: Tingad: Coll. Deckert: [illegible].

**postrufomarginata** (sf)—*Lysandra bellargus rufomarginata postrufomarginata* Verity, 1943—115:296—Syntypes 2♂♂, 6♀♀ [Yugoslavia]: Istria: Portorose: 1-16 IX [19]26: Verity [leg.].

**postschiffermuelleri** (sf)—*Philotes baton schiffermuelleri postschiffermuelleri* Verity, 1943—115:117—Syntypes 12♂♂, 11♀♀ [Greece]: Macedonia: Olympus: 1500-2500 ft.: 14 VII-30 VIII 1935: Romei [leg.].

**postthersites** (sf)—*Lysandra thersites postthersites* Verity, 1934—094:27—Syntypes 1♂, 1♀ [France]: Vendee: Auzay: 20 VIII 1918.

**postzelleri** (sf)—*Polyommatus icarus zelleri postzelleri* Verity, 1943—115:256—Syntypes 1♂, 3♀♀ [Italy: Toscana]: Firenze: Colline di Firenze: 300 m: 8-15 VIII 1920; Pian di Mugnone: 5 VII-17 IX [19]29, 26 VIII [19]40: Querci [leg.].

**praebleusei** (sf, if, ra)—*Palaeoloweia tityrus praebleusei* Verity, 1934—094:17—Syntypes 1♂, 2♀♀ [Spain]: Asturijas: Pajares: 1300 m: 18 VIII [19]24: Romei [leg.].

**praecocior** (sf, if)—*Scolitantides baton praecocior* Verity, 1919—042:29—Syntypes 1♂, 1♀ Italy: Toscana: Firenze: Pian di Mugnone: 200 m: 11-21 IV 1916: Querci [leg.]; specimens remounted and relabelled.

**praelibisonis** (sr, if)—*Lysandra icarius libisonis praelibisonis* Verity, 1943—115:278—N. Italy: Alto Adige.

***praepanoptes** (ra)—*Turania hylas praepanoptes* Verity, 1928—066:143—Syntypes 2♂♂[France]: Pyr[enees-]Orient[ales]: Ambollos: 12 V 1914: Lucas [leg.].

***praeterinsularis** (ra)—*Plebeius insularis praeterinsularis* Verity, 1921—042:175—Syntypes(?) 6♂♂, 3♀♀ Japan: Yokohama.

**prior** (sf)—*Agriades coridon hispana prior* Verity, 1921—042:191.

**pseudocyllarus** (if)—*Polyommatus icarus pseudocyllarus* Verity, 1903—003:288—Holotype ♂ [Italy: Toscana]: Firenze: Lungo il Mugnone: Meta di VI [1]903: [Verity leg.]; type.

***pseudohypochiona** (ra)—*Lycaeides argus pseudohypochiona* Verity, 1931—

081:42—Syntypes 6♂♂, 7♀♀ [France: Var]: Nimes: Ch[amp] de tir: 29 V-7 VI [19]27: Gaillard [leg.].

***pseudolorquinii** (ra)—*Cupido sebrus pseudolorquinii* Verity, 1925—054:76—Syntypes 4♂♂, 3♀♀ [Spain]: Aragon: [Tereul]: Albarracin: 7-23 VI [19]24: Querci [leg.]—Manley & Allcard (1970): *Cupido sebrus pseudolorquinii* [nec Verity], subspecies.

**pulcherrima** (sf)—*Polyommatus icarus celina pulcherrima* Verity, 1919—042:44—Syntypes 82♂♂, 46♀♀ [Italy: Sicily]: Palermo: S. Martino delle Scale: 20 IV-19 V 1918: Querci [leg.]; all specimens remounted and relabelled.

***pulchraphilonome** (ra)—*Lycaeides argus pulchraphilonome* Verity, 1931—081: 67—Syntypes(?) 2♂♂, 8♀♀ [France]: Morbihan: Plouharnel: illegible: 17 VI [19]24; only three specimens carry data label (very poorly legible), data for the rest of the series by implication only.

***pyrenaefuscans** (ra)—*Maculinea arion pyrenaefuscans* Verity, 1948—116:106—Syntpes 5♂♂ [France: Hautes-Pyrenees]: Gedre.

***pyrenaeorum** (ra)—*Lysandra amandus pyrenaeorum* Verity, 1949—116:156—Holotype ♂ [France: Hautes-]Pyrenees: Gedre: VII 1921; 'olotipo': *pyrenaeorum*—Manley & Allcard (1970): *Plebicula amandus pyrenaeorum* [nec Verity], subspecies.

***pyrenemontana** (ra)—*Heodes virgaureae pyrenemontana* Verity, 1929—070:131—Syntypes 10♂♂ [France]: H[autes-]P[yrenees]: Gedre: VII [19]16: Rondou [leg.].

***quercii** (ra)—*Cyaniris semiargus quercii* Verity, 1919—042:45—Syntypes 2♂♂, 1♀ Italia merid.: Calabria: Aspromonte: [Altipiano di Carmelia]: 1200 m: 20 VII 1914: Querci [leg.].

**radiata** (if)—*Chrysophanus alciphron columbanus radiata* Turati & Verity, 1911—015:247—Holotype ♂ [Italy: Alpi Marittime]: Valdieri: 10 VIII [19]09: [Verity leg.]; type: *radiata*.

**RAMBURI** (nn)—*Lycaena ramburi* Verity, 1913—023:189—Replacement name for *Lycaena idas* Rambur, 1842, said to be junior secondary homonym of *Papilio idas* Linnaeus, 1761; the two species are not considered congeneric at present and *ramburi* is at species-rank usually treated as junior subjective synonym of *Aricia morronensis* (Ribbe, 1910).

**rasa** (nomen nudum)—*Polyommatus icarus rasa* Verity, 1920—046:48—Name published without description, definition or indication.

**rasa** (nomen nudum)—*Polyommatus icarus zelleri rasa* Verity, 1920—042:145—Name for subrace published without description, definition or indication.

***rasa** (ra)—*Polyommatus icarus rasa* Verity, 1943—115:249—Holotype(?) ♂ Suditalia: Massiccio delle Mainarde: Valle Mollarino: 500 m: 8 VII 1919: Querci [leg.]; type: *rasa*.

**reverdini** (sf)—*Lycaena aragonensis rezniceki reverdini* Verity, 1916—032:516—Italy: Toscana.

***rondouidimidia** (ra)—*Agriades escheri rondouidimidia* Verity, 1929—071:158—Syntypes 3♂♂, 2♀♀ [France]: Hautes-Pyrenees: Gedre: 26 VII [19]16, VII 1921, 16 VII [19]24: Rondou [leg.].

**rosea** (if)—*Polyommatus icarus rosea* Verity, 1943—115:249—Holotype(?) ♂ [Italy]: Toscana: Alpi Apuane: Monte Matana: VII-VIII [19]01: [Verity leg.].

***rufoclarens** (ra)—*Agriades coridon rufoclarens* Verity, 1926—058:122—Italy: Toscana: Lucca: Fegana Valley.

**rufolunulata** (if)—*Agrodiaetus ripartii rufolunulata* Verity, 1943—115:321—Italy: Alpi Marittime: Mentone: Colle di Castiglione.

***rufoprivata** (ra)—*Polyommats icarus rufoprivata* Verity, 1926—058:106—Syntypes 5♂♂, 1♀ [N. Italy: Torino]: Alpi Cozie: Sestrieres: 2035 m: [peat bogs]: 8 VIII 1925: Verity [leg.].

***rufosaturior** (ra)—*Agrodiaetus damon rufosaturior* Verity, 1943—115:328—Syntypes 10♂♂, 8♀♀ [N. Italy: Torino]: Alpi Cozie: Val Susa: Oulx [= Ulzio]: 1100 m: 13 VII-10 VIII 1925: Verity [leg.].

***rufosplendens** (ra)—*Agriades coridon rufosplendens* Verity, 1926—058:122—Syntypes 66♂♂, 39♀♀ [N. Italy: Torino]: Alpi Cozie: Val Susa: Oulx [= Ulzio]: 1100 m: 7 VII-16 VIII 1925: Verity [leg.].

***ruscinonis** (ra)—*Lysandra coridon ruscinonis* Verity, 1951—116:169—Syntypes 8♂♂, 1♀ [France]: Pyrenees-Orientales: Vernet-les-Bains: ete 1885, ete 1887, VIII 1903, 26 VII-11 VIII 1905, VII-VIII 1906: Oberthür [leg.].

**samsoni** (if)—*Agriades coridon samsoni* Verity, 1920—042:140—Switzerland: Geneva: Gr. Saleve.

***saturior** (ra)—*Plebeius idas saturior* Verity, 1927—063:11—France: Pyrenees-Orientales: Vernet-les-Bains—Manley & Allcard (1970): *Lycaeides idas saturior* [nec Verity], subspecies.

***saxonica** (ra)—*Agriades aragonensis saxonica* Verity, 1919—042:29—Germany: Berlin, Dresden.

***semimontensis** (ra)—*Aricia medon semimontensis* Verity, 1928—067:180—Syntypes 22♂♂ [Spain]: Catalonia: [Montseny]: Santa Fe: 1200 m: 2 VII-6 VIII 1925: Querci [leg.]—Manley & Allcard (1970): *Aricia montensis semimontensis* [nec Verity], subspecies.

**septembris** (sf)—*Agriades hispana rezniceki septembris* Verity, 1923—052:11—Syntypes 37♂♂, 8♀♀ [Italy]: Genova: Quezzi: 28 VIII [1]916, 28 VIII [1]906, 28 VIII [1]913, 23 VIII [1]912, 16 VIII [1]913, 3 IX [1]917, 10 IX [1]905, 13 IX [1]906: Rocci [leg.].

**sesquiopulenta** (sr, if)—*Lycaeides idas opulenta sesquiopulenta* Verity, 1943—115:175—Syntypes 1♂, 3♀♀ [N. Italy]: Lago Maggiore: Intra: 200 m: 6-7 IX [19]28, 28 VIII [19]40: [Verity leg.].

**sesquiviola** (if)—*Palaeochrysophanus hippothoe mirus sesquiviola* Verity, 1943—115:70—Syntypes 2♂♂, 1♀ [Austria]: Carinthia: Glockner: 2000 m: 15 VII-13 VIII 1927: Coll. Zuellich.

***sibyllina** (ra)—*Lycaena coridon sibyllina* Verity, 1916—029:133—Syntypes 38♂♂, 36♀♀ Italy: Marche: Piceno: Monti Sibillini: Bolognola: 1200 m: 1 VII-1 IX 1910: Querci [leg.]; all specimens remounted and relabelled.

***sicca** (ra)—*Agriades escheri sicca* Verity, 1929—071:159—Syntypes 6♂♂, 2♀♀ [France]: Loz[ere-et-]Avey[ron]: La Rozier: to 1800 ft.: 10-15 VII 1926: Graves [leg.]; Peyreleans: Chausse Noir: to 2500 ft.: 10-15 VII 1926: Graves [leg.].

**simplicior** (if)—*Lampides telicanus simplicior* Verity, 1911—016:273—Italy: Modena—Type material (holotype only) destroyed by museum pests.

***sophiana** (ra)—*Lycaeides argus sophiana* Verity, 1931—081:60—Syntypes 2♂♂, 1♀ [Bulgaria]: 10 km W. of Sophia: Lulin: 2700 ft.: 22 VII [19]27: [Graves leg.].

**splendida** (nomen nudum)—*Agriades thetis splendida* Verity, 1919—042:31—Name for race published without description, definition or indication and attributed to Stefanelli, later treated by Verity (042:43) as incorrect subsequent spelling of *Lycaena escheri splendens* Stefanelli, 1904.

**squalida** (if, ra)—*Polyommatus meleager squalida* Verity, 1920—042:145—Syntypes 6♂♂, 3♀♀ Italia centrale: Marche: Piceno: Bolognola: Massiccio Sibillini: 1200 m: 18 VII-22 VIII 1918: Querci [leg.]; original rank confused: individual form of female and race.

**stefanellii** (if)—*Lycaena coridon stefanellii* Verity, 1904—006:11—Holotype ♀ [Italy: Toscana]: Firenze: Verity [leg.]; type: *stefanellii.*

**styx** (if)—*Lycaena escheri styx* Turati & Verity, 1911—015:258—Holotype ♀ [Italy: Alpi Marittime]: Valdieri: 15 VII [19]11: [Verity leg.].

***subcalida** (ra)—*Aricia medon subcalida* Verity, 1920—042:150—Syntype 1♂ Italia centrale: Lucca: Fiume Fegana: 500 m: 15 VIII 1915: Querci [leg.].

***subcanariensis** (ra)—*Aricia cramera subcanariensis* Verity, 1928—067:183—Syntypes 5♂♂, 1♀ [Spain]: Aragon: [Teruel]: Albarracin: 1100 m: 25 VI-30 VII [19]24: Querci [leg.].

***subcramera** (ra)—*Aricia cramera subcramera* Verity, 1928—067:182—Syntypes 3♂♂, 2♀♀ [Spain]: Andalucia: Sierra Nevada: 1200 m: 11-28 V [19]26: Querci [leg.]—Manley & Allcard (1970): *Aricia cramera subcramera* [nec Verity], subspecies.

**subornata** (sf)—*Aricia medon subornata* Verity, 1920—042:148—Italy: Firenze: Pian di Mugnone.

***subpauper** (ra)—*Glaucopsyche cyllarus subpauper* Verity, 1928—066:142—Syntypes 6♂♂, 4♀♀ [France: Var]: Cannes, Nimes: Ch[amp] d[e] tir: 11 IV [19]26, 29 V [19]24, 6 VI [19]26: Gaillard [leg.].

**subradiosa** (if)—*Lysandra albicans florentina subradiosa* Verity, 1943—115:306—Holotype ♀ Italia centrale: Firenze: Pian di Mugnone: 200 m: 16 VI 1915: Querci [leg.].

***subsaturior** (ra)—*Lycaeides idas subsaturior* Verity, 1948—116:110—Syntypes 4♂♂ [France: Pyrenees-Orientales]: Ariege: Morens: 1000-1800 m: 10 VII [19]31, Ariege: Aix-les-Thermes: VIII 1927, Gard: Massif Aigoual: Hort Dien: 20 VIII [19]26, 9 VIII [19]30: [all] Coll. Stempffer.

**suffescens** (if)—*Lysandra thersites suffescens* Verity, 1943—115:271.

***superapennina** (ra)—*Lycaena coridon superapennina* Verity, 1916—029:131—Italy: Toscana: Lucca: Mt. Pratofiorito: 900 m.

**superlunulata** (if)—*Polyommatus meleager alpium superlunulata* Verity, 1926—058:121—Italy: Alpi Cozie: Ulzio.

**supraddenda** (if)—*Maculinea arion supraddenda* Verity, 1943—115:152—Holotype ♀ [Italy]: Modena: M. Gibbio: Candal [illegible]: 12 VII [19]08: Costnatini [leg.]; 'olotipo': *supraddenda.*

***tapinaegus** (ra)—*Lycaeides argyrognomon tapinaegus* Verity, 1948—116:117—Syntypes 2♂♂ [France]: Charente: Monthiers s. Boeme: 27-28 VII 1921.

**transferens** (nomen nudum)—*Polyommatus icarus zellerica transferens* Verity & Querci, 1924—052:45—Name for seasonal form published without description, definition or indication.

**transferens** (sf)—*Polyommatus icarus zelleri transferens* Verity, 1943—115:257—Syntypes 5♂♂, 3♀♀ [Italy: Toscana]: Firenze: Pian di Mugnone: 15-20 VII 1940, 16 X 1940, 13-26 X [19]27, 6 X [19]29, 30 X [19]32, 6 XI [19]32.

**TRAPPI** (nn)—*Plebeius sephyrus trappi* Verity, 1927—063:16—Replacement name for *Lycaena sephyrus lycidas* Trapp, 1863 said to be secondary junior homonyn of *Polyommatus lycidas* Meigen, 1830; the two taxa are not congeneric.

***trinacriae** (ra)—*Cupido minimus trinacriae* Verity, 1919—042:47—Syntypes 7♂♂, 5♀♀ [Italy]: Isola di Sicilia: Palermo: Monreale: San Martino: 800 m: 24 IV-12 V 1918: Querci [leg.]—Higgins & Riley (1970): *Cupido minimus trinacriae* [nec Verity], subspecies.

**TURATIANA** (nn)—*Lycaena euphemus turatiana* Verity, 1923—052:7—Replacement name for (possible available name) *Lycaena alcon italica* Turati, 1919, said to be preoccupied by *Lycaena tithonus italica* Oberthur, 1910.

***turatii** (ra)—*Agriades escheri turatii* Verity, 1919—042:31—Syntypes 4♂♂, 2♀♀ [Italy]: Parma: Salsomaggiore: VI [18]96: [Turati leg.].

***tuscanica** (ra)—*Plebeius argus tuscanica* Verity, 1919—042:45—Syntypes 10♂♂, 2♀♀ [Italy: Toscana: Pisa]: Casciana: 3 VIII 1913; specimens remounted and relabelled.

**ultima** (sr)—*Plebeius idas australissima ultima* Verity, 1927—063:13—Syntypes 5♂♂, 2♀♀ Suditalia: Massiccio delle Mainarde: Valle Mollarino: 500 m: 30 VI-18 VII 1919: Querci [leg.].

***ultraornata** (ra)—*Scolitantides orion ultraornata* Verity, 1937—107:72—Syntypes 8♂♂, 6♀♀ Finlandia: Sortavala: Riekkalansaari: 26 V-6 VI 1936: Brandt leg.

***ultragordius** (ra)—*Loweia alciphron ultragordius* Verity, 1926—058:105—N. Italy: Alpi Cozie: Ulzio—Beuret (1953): *Heodes alciphron ultragordius* [nec Verity], subspecies.

**upoleuca** (if)—*Chrysophanus dorilis upoleuca* Verity, 1904—004:58—Holotype ♂ [Italy]: Modenese: Monte Gibbio: 22 V [1]903; type: *upoleuca*.

**VALDERIANA** (ssp)—*Chrysophanus hippothoe valderiana* Turati & Verity, 1911—015:243—Syntypes 12♂♂, 6♀♀ [Italy: Alpi Marittime]: Valdieri: VII: [Verity leg.].

**varieleus** (nomen nudum)—*Rumicia phlaeas varieleus* Verity, 1920—042:5—Name for race published without description, definition or indication.

**varieleus** (ra, sf)—*Lycaena phlaeas varieleus* Verity, 1943—115:57—Italy: Alpi Marittime: Terme di Valdieri: 1400 m—Said to inhabit only the warmest alpine valleys in summer, i.e. as seasonal form of gen. 2, implied to race.

**vectae** (nomen nudum)—*Agriades thetis vectae* Verity, 1919—042:29—Name proposed in the subheading and published without description, definition or indication; misspelling of *vestae* (cf. 042:43).

**veris** (if)—*Plebeius argus veris* Verity, 1924—053:110—Syntypes 1♂, 2♀♀ Italia centrale: Lucca: Valle Camaione: 300 m: 3-8 VI 1923: Querci [leg.].

***vestae** (ra)—*Agriades thetis vestae* Verity, 1919—042:30—Syntypes 15♂♂, 1♀ [England]: Isle of Wight: Ventnor: 30 V 1875: Conquest [leg.].

**violacea** (if)—*Lycaena sebrus violacea* Verity, 1911—016:277—Hologype ♀ [Italy]: Modenese: Monte Gibbio: 22 V[1]903; type: *violacea.*

**virescens** (if)—*Lysandra argester virescens* Verity, 1943—115:281.

***virgatus** (ra)—*Callophrys rubi virgatus* Verity, 1913—023:187—Syntypes 22♂♂, 13♀♀ Italy: Toscana: Firenze: Pian di Mugnone: 200 m: 12 IV-16 V 1911: Verity [leg.]; all specimens remounted and relabelled.

***zelleri** (nn)—*Polyommatus icarus zelleri* Verity, 1919—042:44—Replacement name for unavailable infrasubspecific name of aberration *Polyommatus icarus meridionalis* Tutt, 1910, said to be preoccupied by another subspecies-rank name of varietas *Agriades coridon meridionalis* Tutt, 1910; Verity treated *zelleri* as race. Larsen (1974): *Polyommatus icarus zelleri* [nec Verity], subspecies.

**zellerica** (nomen nudum)—*Polyommatus icarus zellerica* Verity & Querci, 1924—052:45—Name for race published without description, definition or indication; apparently incorrect subsequent spelling of *Polyommatus icarus zelleri* Verity, 1919.

## RIODINIDAE

**latevittata** (if)—*Hamearis lucina latevittata* Verity, 1943—115:388.

***parvifulvior** (ra)—*Nemeobius lucina parvifulvior* Verity, 1923—052:14—Syntypes 2♂♂, 1♀ [England: Suffolk]: Ipswich: Belstead Wood; all specimens under group-label.

***praestans** (ra)—*Nemeobius lucina praestans* Verity, 1923—052:13—Syntypes 3♂♂, 1♀ Italia centr.: Toscana: Firenze: Fosca Vignone: 100 m: 5-25 V 1919: Querci [leg.].

## PAPILIONIDAE

***abetonica** (ra)—*Parnassius apollo abetonica* Verity, 1947—117:94—Syntypes 14♂♂, 14♀♀ [Italy: Toscana]: Appennino pistoiese: Abetone: 1400 m: 14-28 VII [19]29—Name proposed for 'local form'.

**aestivoides** (sf)—*Papilio machaon aestivoides* Verity, 1919—043:88—Syntype 1♂ [S.W. France]: Vendee.

**albina** (if)—*Parnassius apollo albina* Verity, 1911—010:312—Name published in synonymy of *P. apollo isabellina* Oberthür, 1909.

**albomaculata** (if)—*Papilio syphanius albomaculata* Verity, 1907—010:108—N.W. China: Ta-tong-kiao.

**albopruinosa** (nn)—*Parnassius apollo albopruinosa* Verity, 1947—117:94—Replacement for unavailable infrasubspecific name *P. apollo albina* Osthelder, 1925 which Verity considered junior homonym of *P. apollo albina* Verity, 1911.

**alpestris** (fm)—*Parnassius delius intermedius alpestris* Verity, 1911—010:314—[U.S.S.R.: Altay Mts.]: Tchuja Valley: [Elwes leg.].

**alpica** (ra)—*Papilio machaon machaon alpica* Verity, 1911—010:295—Syntypes 1♂, 1♀ [N. Italy]: Piemonte: Alpi Maritime: Valdieri: VII [18]98.

**ampliusmaculata** (ab)—*Parnassius apollo ampliusmaculata* Verity, 1911—010: 311—Sweden: Naes Vek.

**amurensis** (ra)—*Papilio machaon hyppocrates amurensis* Verity, 1911—010:292—[U.S.S.R.: Far East: Amur]: Pokrokofka, Chabarofka, Raddefka—Eller (1936): *Papilio machaon amurensis* [nec Verity 1911], subspecies.

**amurensis** (ra)—*Parnassius stubbendorfi stubbendorfi amurensis* Verity, 1911—010:321—[U.S.S.R.: Far East]: Amur, Vladivostok.

**angulata** (ra)—*Papilio machaon machaon angulata* Verity, 1911—010:296—Morocco: Tanger.

**apollodelius** (hy, ab)—*Parnassius apollodelius* Verity 1911—010:312—[Switzerland]: Engadin—Name for hybrid of *P. apollo* (Linnaeus, 1758) with *P. phoebus* (Fabricius, 1793) or aberration of *P. apollo.*

**atava** (ab)—*Papilio feisthameli atava* Verity, 1911—010:293—Name for specimen figured by Oberthür (1909) in Etud. Lepid. Comp. 3:108, pl. XXIV, fig. 124.

**attica** (ra)—*Papilio alexanor alexanor attica* Verity, 1911—010:294—Syntypes 2♂♂ Graecia: Attica: [illegible].

**avinoffi** (ra)—*Parnassius simo simo avinoffi* Verity, 1911—010:316—Hindukush: Beik: 5000 m.

**bartholomaeiformis** (if)—*Parnassius apollo pumilus bartholomaeiformis* Verity, 1915—028:205—Syntype ♀ [Italy]: Aspromonte: Montalto: 1600 m: 12-25 VII [1914]; *bartholomaeiformis*: 'olotipo'.

**bigenerata** (nomen nudum)—*Papilio machaon bigenerata* Verity, 1919—042:88—Name published without description, definition or indication.

**bigenerata** (ra, sf)—*Papilio machaon bigenerata* Verity, 1947—117:31—Syntype 1♂ [C. Europe]: 17 V 1918; 'Type: 1. gen. nominale della *bigenerata* Vrty.'

**caeca** (ab)—*Parnassius delphius staudingeri caeca* Verity, 1911—010:317—[C. Asia]: Buchara: Ljagara Murda.

**cassandraclara** (sr, sf)—*Zerynhthia hypsipyle cassandra cassandraclara* Verity, 1947—117:60—Syntypes 3♂♂, 1♀ [Yugoslavia]: Croatia: Podsused: IV 1909, Zagobria [= Zagreb]: 5 V 1909.

**caucasia** (ra)—*Parnassius mnemosyne mnemosyne caucasia* Verity, 1911—010: 320—Syntypes 3♂♂ [U.S.S.R.]: Caucas[us]: Kub[an] Geb[iet]: 10 VII [19]02: coll. Bartel.

**chinensis** (ra, sf)—*Papilio machaon hippocrates chinensis* Verity, 1907—010:108—China: Szechwan: Traku, Venchuah—Eller (1936): *Papilio machaon chinensis* [nec Verity 1907], subspecies.

**chitralica** (ra)—*Parnassius deplphius hunza chitralica* Verity, 1911—010:317—[Pakistan]: Chitral: Baroghil Valley: 3600 m—Talbot (1939): *Parnassius delphius chitralica* [nec Verity 1911], subspecies.

**chryseis** (ab)—*Parnassius apollo chryseis* Verity, 1907 [nec Oberthür] 010:103—[U.S.S.R.]: Turkestan: Fort Naryn.

**confluens** (ab)—*Papilio podalirius confluens* Verity, 1911—010:292—[Germany]: Dresden: Blasewitz.

**creta** (ra)—*Papilio podalirius creta* Verity, 1911—010:292—Greece: Athens.

**cypria** (ra)—*Papilio machaon machaon cypria* Verity, 1908—010:13—Cyprus: Larnaca.

**decoratissima** (if, ra)—*Parnassius apollo decoratissima* Verity, 1919—042:88—Syntypes 5♂♂, 4♀♀ Italia centrale: [Toscana]: Lucca: Prato Fiorito: 1000 m: 2 VII 1901, 27-28 VII 1915, 6 VIII 1915: Querci, Verity [leg.].

**deminuta** (sr)—*Zerynthia hypsipyle creusa deminuta* Verity, 1947—117:57—Syntypes 2♂♂, 3♀♀ [France: Alpes-Maritimes]: St. Barnabe: 11 V [19]34, 8 IV [19]37: J. Gazel; [Italy]: Croatia: Triest: 16-30 II [19]11, 8 IV [????]: H. Stauder.

**diaphana** (ab)—*Parnassius delphius diaphana diaphana* Verity, 1907—010:78—[China]: Szechwan: Tatsienlou.

**dubia** (ab)—*Parnassius dicobolus discobolus dubia* Verity, 1907—010:108—[U.S.S.R.: C. Asia]: Boro-Choro Mts.

**dubitabilis** (fm)—*Parnassius actius actius dubitabilis* Verity, 1911—010:313—Syntype ♂ [U.S.S.R.]: Karagaitau.

**elongata** (ra)—*Papilio podalirius elongata* Verity, 1911—010:292—[Romania]: Hongrie: Herculesbad.

**emihippocrates** (ra)—*Papilio machaon machaon emihippocrates* Verity, 1911—010:296—Nepal—Talbot (1939): *Papilio machaon emihippocrates* [nec Verity], subspecies.

**emisphyrus** (sf, ra)—*Papilio machaon emisphyrus* Verity, 1919—042:88—Syntypes 1♂, 1♀ [Italy]: Firenze: [illegible]: 8 V [19]08, 4 V [19]17.

***euappenninus** (ra)—*Parnassius apollo euappenninus* Verity, 1915—028:204—Syntypes 12♂♂ Italia centrale: Piceno: Monti Sibillini: 1800-1900 m: 20 VII-3 VIII 1913: Querci leg.; all remounted and relabelled.

**excelsa** (ra)—*Parnassius mnemosyne mnemosyne excelsa* Verity, 1911—010:320—Switzerland: high summits: mt. Cenis: 2100 m.

**feisthamelides** (hy, ab)—*Papilio feisthameli festhamelides* Verity, 1911—010:293—Spain: Granada: mountains.

**flavescens** (fm)—*Doritis apollinus flavescens* Verity, 1907—010:108—Asia Minor.

**flavoinspersa** (ab)—*Papilio hospiton flavoinspersa* Verity, 1911—010:295—[France]: Corsica: Calacuccia: Luri: Evisa: V-VI [????].

**flavomaculata** (ab)—*Thais cerisyi cerisyi flavomaculata* Verity, 1905—010:31—[Turkey]: Pont: Amasia.

**gigantea** (ra)—*Papilio machaon machaon gigantea* Verity, 1911—010:295—Greece, Dalmatia—Eller (1936): *Papilio machaon giganteus* [nec Verity], subspecies.

**glocnerica** (ra)—*Parnassius apollo glocnerica* Verity, 1911—010:310—[Austria]: Grossglockner.

**halteres** (ab)—*Parnassius mnemosyne mnemosyne halteres* Verity, 1907—010:99—Authorship uncertain, probably erroneously attributed to Muschamp.

**helvetica** (nomen nudum)—*Parnassius mnemosyne mnemosyne helvetica* Verity, 1911—010:320—Name for race published without description, indication or definition.

**hippocratides** (sf)—*Papilio machaon hyppocrates hippocratides* Verity, 1908—010:16—Syntype 1♀ Japan—Spelled also *hyppocratides.*

**immaculatus** (fm)—*Papilio machaon zolicaon immaculatus* Verity, 1905—010: 18—Cyprus: Larnaca—Original combination confused and uncertain.

**inalpina** (ra)—*Papilio podalirius inalpina* Verity, 1911—010:291—[Switzerland]: Engadin: Tarasp.

**inornata** (if)—*Thais hypermnestra cassandra inornata* Verity, 1919—042:88—Syntype ♀ Italia centrale: Toscana: Firenze: Fosso Vinpore: 100 m: 4 V 1919: Querci [leg.]; f. *inornata* Vrty.

**interjecta** (ra)—*Papilio podalirius interjecta* Verity, 1911—010:291—Syria: Akbes; Morocco.

**interjecta** (ra)—*Parnassius delphius delphius interjecta* Verity, 1911—010:316—[U.S.S.R.]: Transalai.

**intermedia** (ra)—*Hypermnestra helios intermedia* Verity, 1911—010:301—Syntypes 1♂, 1♀ [U.S.S.R.: C. Asia]: Syr Darja: Aj-Darle: 12 IV 1909: Koshantschikoff [leg.].

**joannisi** (ra)—*Papilio machaon orientis joannisi* Verity, 1905—010:12—Syntype ♂ (Holotype?) [U.S.A.]: Alaska: Nualto: 16 VI 1901.

**juldusica** (ra)—*Parnassius delphius infernalis juldusica* Verity, 1911—010:316—East Tian-shan Mts.

**KOREANA** (ssp)—*Parnassius stubbendorfi koreana* Verity, 1907—010:101—Korea.

**lapponica** (ra)—*Papilio machaon machaon lapponica* Verity, 1911—010:296—Lappland: Knoblock.

**latevittata** (if)—*Papilio machaon machaon britanicus latevittata* Verity, 1911—010:295—England: Cambridge: Wicken.

**latevittata** (ra)—*Thais hypermnestra latevittata* Verity, 1919—042:88—Sicily.

**leechi** (ra)—*Papilio feisthameli leechi* Verity, 1911—010:293—Asia Minor.

**luctifera** (ab)—*Parnassius apollo luctifera* Verity, 1911—010:311—Switzerland: Mt. Saleve: 1000 m.

**machaonides** (ab)—*Papilio hospiton machaonides* Verity, 1908—010:10—Corsica.

**magna** (ra)—*Papilio alexanor alexanor magna* Verity, 1911—010:294—Syntype ♀ [Yugoslavia]: Dalmatia: Gravosa: coll. M. Bartel.

**maura** (sf)—*Papilio feisthameli maura* Verity, 1911—010:293—Syntypes 2♂♂ [Algeria]: Alger.

**mauretanica** (ra)—*Papilio machaon machaon mauretanica* Verity, 1908—010: 12—Syntypes 3♂♂ [Algeria]: Alger: IX [18]83—Spelled also *mauritanica*—Eller (1936): *Papilio machaon mauretanicus* [nec Verity], subspecies.

**maxima** (ra)—*Papilio machaon machaon maxima* Verity, 1911—010:296—Syntype ♂ [Morocco]: Tanger.

**melanica** (fm)—*Parnassius delius intermedius melanica* Verity, 1911—010:314—[U.S.S.R.]: Altai: Kuraipan: 2100 m.

**microcreusa** (sr)—*Zerynthia hypsipyle creusa microcreusa* Verity, 1947—117: 57—Syntype ♀ [France]: Var: Roquebrune: 31 III [19]41: Quiberteau [leg.].

**microsphyroides** (sr, sf)—*Papilio machaon emisphyrus microsphiroides* Verity, 1947—117:28—Syntypes 2♂♂, 1♀ [Italy]: Abruzzi: Sirente: Monterotondo: 1500 m: 8 IX [19]41.

**minuscula** (fm)—*Parnassius apollo minuscula* Verity, 1911—010:312—Dourbes.

**minuta** (ra)—*Parnassius actius actius minuta* Verity, 1911—010:313—Syntypes 1♂, 1♀ [U.S.S.R.: C. Asia]: Juldus [Mts.].

***nemorensis** (ra)—*Thais hypermnestra nemorensis* Verity, 1919—042:88—Syntypes 5♂♂, 1♀ [Italy: Toscana: Lucca]: Forte dei Marmi: 14 V [1]901, 9 IV [19]12: [R. Verity leg.].

**nevadensiformis** (if)—*Parnassius apollo pumilus nevadensiformis* Verity, 1915—028:205—Syntype ♀ [Italy]: Aspromonte: Montalto: 1600 m: 12-25 VII [1914].

**nexa** (ra)—*Parnassius discobolus discobolus nexa* Verity, 1911—010:313—Korla.

**nigerrima** (ab)—*Parnassius delius smintheus nigerrima* Verity, 1907—010:108—[Canada]: British Columbia: Rocheoses Mts.

**nigrescens** (ab)—*Papilio podalirius nigrescens* Verity, 1911—010:292.

**nigroinspersa** (ab)—*Parnassius simo simulator nigroinspersa* Verity, 1907—010:108—E. Turkestan: Ak-sou.

**nigrosquamosa** (if)—*Parnassius phoebus serenus nigrosquamosa* Verity, 1947—117:74—Syntype ♀ [Italy]: Alpi Cozie: Sestrieres: 2035 m: 8 VIII 1925: Verity [leg.].

**nigrovenata** (ab)—*Papilio podalirius nigrovenata* Verity, 1908—010:5—[Turkey]: Asia Minor: Brousse [= Brusa].

**obliterata** (ab)—*Parnassius delphius stoliczkanus obliterata* Verity, 1911—010:317—Koulou.

**obscurata** (fm)—*Parnassius bremeri bremeri obscurata* Verity, 1911—010:303—[U.S.S.R.: Far East]: E. Amur: Raddefka.

**ocellata** (fm)—*Parnassius delius intermedius ocellata* Verity, 1907—010:108.

**ochracea** (ab)—*Hypermnestra helios ochracea* Verity, 1907—010:108—[U.S.S.R.: C. Asia]: Namanghan.

**orientalis** (ra)—*Parnassius mnemosyne gigantea orientalis* Verity, 1911—010:321—[U.S.S.R.]: Alexander Mts.

**ORIENTIS** (ssp)—*Papilio machaon orientis* Verity, 1911—010:297—Syntypes 3♂♂, 1♀ [U.S.S.R.]: Sayan: Tounkoun [= Tonkun]; material from Mongolia: Changai; Irkutsk and Amur: Pokrokofka not examined.

***oulxensis** (ra)—*Parnassius apollo oulxensis* Verity, 1926—058:175—Syntypes 12♂♂, 14♀♀ [N.W. Italy]: Alpi Cozie: Val Susa: Oulx [= Ulzio]: 1100 m: 5 VII-16 VIII 1925: Verity [leg.].

**perfusa** (ab)—*Parnassius apollo perfusa* Verity, 1911—010:312—Tyrol.

**persica** (ra)—*Papilio podalirius persica* Verity, 1911—010:291—[Iran]: Perse: Gulhak.

**plenissima** (sf)—*Iphiclides podalirius valesiaca plenissima* Verity, 1926—058:176—Syntypes 1♂, 1♀ [N. Italy]: Südtirol: [Meran]: 324 m: [6 V 1917].

**posticelongata** (ab)—*Parnassius apollo pumilus posticelongata* Verity, 1915—028:204—Syntype ♂ [Italy]: Aspromonte: Montalto: [1600 m]: 12-25 VII [1914].

**posticemaculata** (ab)—*Parnassius phoebus posticemaculata* Verity, 1947—117:68—Italy: Trentino: Val di Genova: Malga Bedole: Fiori [leg.].

**pseudodelius** (ab)—*Parnassius apollo pseudodelius* Verity, 1911—010:312—Italy: Piemonte: [Alpi Maritime]: Valdieri: 1400 m.

**pseudodelius** (if)—*Parnassius apollo valderiensis pseudodelius* Turati & Verity, 1911—015:188—Type-material destroyed by museum pests.

**pseudonubilosus** 9ra)—*Parnassius mnemosyne nubilosus pseudonubilosus* Verity, 1911—010:321—[Turkey]: Asia Minor: Pont: Trebizonde; Persia.

**redivivigigas** (ra)—*Parnasius apollo redivivigigas* Verity, 1947—117:91—Syntypes 16♂♂, 13♀♀ [italy]: Alpi Pennine: Valle Anzasca: Vanzone: 700 m: 20-25 VI [19]24, 11-25 VII [19]24, VI [19]25, 17-26 VII [19]24: [Verity leg.].

**revertens** (nomen nudum)—*Papilio machaon sphyrus revertens* Verity, 1924—052:23—Name for seasonal form published without description, definition or indication.

**revertens** (sf)—*Papilio machaon sphyrus revertens* Verity, 1947—117:27—Syntype 2♀♀ [Italy: Sicily]: Palermo: Trabia: [50 m]: X [1]930.

***romeii** (ra)—*Parnassius apollo romeii* Verity, 1939—110:182—Syntypes 1♂, 3♀♀ [Italy]: Abruzzi: Gran Sasso: 1600-1700 m: 27 VII-13 VIII 1939: L. Romei [leg.].

**rothschildi** (ra)—*Parnassius apollo rothschildi* Verity, 1911—010:310—Italy.

**rotundata** (fm)—*Parnassius discobolus discobolus rotundata* Verity, 1911—010: 312—[N.W. China]: Kuldja: Boro Koro.

**separanda** (fm)—*Parnassius actius actius separanda* Verity, 1911—010:313—Syntype 1♀ Karagai-tau.

**septentrionalis** (ra)—*Papilio machaon hyppocrates septentrionalis* Verity, 1911—00:299—Japan: Hokkaido: Sapporo, Hakodate.

**septentrionalis** (ra)—*Parnassius eversmanni septentrionalis* Verity, 1911—010: 319—[U.S.S.R.]: N.E. Sibiria: Wittim, Vilui.

**sikkimensides** (fm)—*Papilio machaon machaon sikkimensides* Verity, 1911—010:296—S. Kashmir: Pangi.

**sphyroides** (fm)—*Papilio machaon machaon sphyrus sphyroides* Verity, 1908—010:12—[Mediterranean].

**subdiaphana** (fm)—*Parnassius eversmanni subdiaphana* Verity, 1907—010:94—[U.S.S.R.]: Jakoutsk.

**subdiaphana** (fm)—*Parnassius simo simulator subdiaphana* Verity, 1907—010: 108—[China]: Lob-nor: Altyn-tag Mts.

**syra** (ra)—*Parnassius mnemosyne nubilosus syra* Verity, 1911—010:321—Syria: Hermon: 1800 m—Larsen (1974): *Parnassius mnemosyne syra* [nec Verity], subspecies.

**syriaca** (ra)—*Papilio machaon machaon syriaca* Verity, 1908—010:13—Syntype 1♂ Syria—Eller (1936): *Papilio machaon syriacus* [nec Verity], subspecies.

**TATSIENLUICA** (ssp)—*Parnassius jacquemonti tatsienluica* Verity, 1906—010: 63—Syntypes 6♂♂, 1♀ [W. China: Szechwan]: Ta-Tsien-Lou: Chasseurs indigenes du P. Dejean: 1903, 1904.

**tenuicincta** (ab)—*Parnassius apollo tenuicincta* Verity,1911—010:311—Italy: Bolzano.

**tersa** (if)—*Parnassius phoebus sacerdos tersa* Verity, 1947—010:71—Syntype ♀ [N. Italy: Südtirol]: Sulden: Ortler: 1800 m: 3-10 VIII [19]20: Verity [leg.].

**tertiana** (sf)—*Papilio machaon tertiana* Verity, 1935—094:49—N. Italy: Anzasca Valley.

**VALDERIENSIS** (ssp)—*Parnassius apollo valderiensis* Turati & Verity, 1911—015:181—Syntypes 6♂♂, 6♀♀ [N. Italy: Piemonte: Alpi Maritime]: Valdieri: [Gesso da St. Anna]: 950 m: 23 VII-15 VIII 1909: [Verity leg.]—All remounted and relabelled—True date of publication apparently 31 XII 1911.

**valderiensis** (ra)—*Parnassius apollo valderiensis* Verity, 1911—010:306—Data as for subspecies *Parnassius apollo valderiensis* Turati & Verity, 1911—Date of publication [31] I 1911.

**valesiaca** (ra)—*Papilio podalirius valesiaca* Verity, 1911—010:291—Switzerland: Wallis: Martigny: Sitten.

**vernus** (nomen nudem)—*Papilio sinon vernus* Verity, 1913—023:176—Name for seasonal form published without description, definition or indication.

**zanclaeides** (nomen nudum)—*Papilio podalirius zancleides* Verity, 1911—010: 291—Name for seasonal form published without description, definition or indication.

## PIERIDAE

**acuminata** (ab)—*Colias chrysotheme chrysotheme schugurovi acuminata* Verity, 1909—010:272—[U.S.S.R.]: S. Russia: Poltava.

**acuminata** (if)—*Euchloe ausonia cuminata* Verity, 1947—117:159—[Italy]: Liguria: Genova, San Remo.

***acuta** (ra)—*Leptosia sinapis acuta* Verity, 1922—042:90—Austria: various localities.

**aegra** (ab)—*Colias myrmidone aegra* Verity, 1909—010:265.

**aegra** (ab)—*Colias croceus aegra* Verity, 1909—010:270—France: Perpignan.

**aegra** (ab)—*Colias hyale aegra* Verity, 1947—117:262—Syntype ♂ Italia centrale: Toscana: Firenze: Pian di Mugnone: 200 m: 23 IV 1918: Querci [leg.].

**aegyptiaca** (ra)—*Euchloe belia belia aegyptiaca* Verity, 1911—010:337—Egypt: Wadi Hof Heluan.

**aestiva** (fm)—*Colias chrysotheme chrysotheme aestiva* Verity, 1909—010:272—Hungary.

**aestiva** (fm)—*Pieris napi euroientis pseudomelete aestiva* Verity, 1911—010:332—Japan: Yezo [= Hokkaido]: Nemoro.

**aestivalis** (fm)—*Euchloe tagis insularis aestivalis* Verity, 1908—010:184—[France]: Corsica.

**aestivus** (nomen nudum)—*Pieris rapae aestivus* Verity, 1913—023:178—Name for seasonal form published without description, definition or indication.

**alba** (ab)—*Colias viluiensis alba* Verity, 1909—010:251—[U.S.S.R.]: N.E. Sibiria: Lena River Basin.

**alba** (ab)—*Colias chrysotheme chrysotheme alba* Verity, 1909—010:273—Austria: Wien: Mödling.

**albescens** (ab)—*Euchloe belia albescens* Verity, 1908 [nec Oberthür]—010:178—[France]: Villenueve de Blaye.

**albescens** (nomen nudum)—*Gonepteryx rhamni albescens* Verity, 1919—042:48—

Name for individual form published without description, definition or indication.

**albescens** (ab)—*Gonepteryx rhamni transiens albescens* Verity, 1947—117:303—[Italy]: Firenze: Giocoli: Collazzi: 300 m.

**albula** (ab)—*Gonepteryx cleopatra europaeus albula* Verity, 1947—117:297—Syntypes 1♂, 1♀ [Italy: Toscana]: Firenze: Via Massaccio: VI [1]923; Costa Toscana: Montenero: 200 m: 8 VII [19]28; Verity [leg.].

**alexandrina** (ra)—*Colias staudingeri alexandrina* Verity, 1909—010:242—Alexander Mts.

**alpestris** (ra)—*Pieris melete melete alpestris* Verity, 1908—117:166—[China]: W. Szechwan: Tatsienlu: Patsefang.

**alpina** (ra)—*Colias aurora alpina* Verity, 1911—010:357—Mongolia: Changai, Kentei.

***alpium** (ra)—*Anthocharis euphenoides alpium* Verity, 1926—058:171—[Italy]: Alpi Cozie: Oulx: V-VI, Cesana: VII.

***alpiumnitida** (ra)—*Colias phicomone alpiumnitida* Verity, 1926—058:171—Syntypes 7♂♂, 4♀ [Italy: Alpi Maritime]: Valdieri: Vallasco: 1700 m: 25 VII 1909, 23 VII 1911, 27 VIII 1911: Verity [leg.].

**ALPHERAKYI** (nn)—*Pieris alpherakyi* Verity, 1907—010:122—Replacement name for *Aporia potanini* Alpheraky 1889 said to be secondary junior homonym of *Pieris potanini* Alpheraky 1888; this case of secondary homonymy resulted from Verity's treatment of *Aporia* Hübner [1819] as a subgenus of *Pieris* Schrank 1801; both taxa are no longer considered congeneric.

**alpigena** (ra)—*Pieris manni alpigena* Verity, 1911—010:336—[Italy]: Aosta.

**alpina** (ra)—*Pieris chloridice chloridice alpina* Verity, 1911—010:328—Ladakh: Chonging Valley: 4500-5100 m.

**altaica** (ra)—*Colias hyale hyale altaica* Verity, 1911—010:348—[U.S.S.R.]: Altay Mts.: Tchuja Valley, Biga Valley.

**altapennina** (sr, if)—*Pieris mannii rossii altapennina* Verity, 1947—117:227—Syntypes 9♂♂, 6♀♀ [Italy]: Firenze: Vallombrosa: 900 m: VIII [19]05, 27 VII-12 VIII [19]31: R. Verity [leg.].

**alterelbursina** (sf)—*Pieris ergane elbursina alterelbursina* Verity, 1937—108:8—Syntypes 3♂♂, 1♀ Iran: [Teheran]: Elbursgebirge: Keredj: 1500 m: 25 V 1936: Brandt leg.

**amdensis** (ra)—*Pieris callidice amdensis* Verity, 1911—010:327—[N. China]: Amdo.

**amdensis** (ra)—*Colias hyale poliographus amdensis* Verity, 1911—010:348—[N. Chna]: Amdo, Kuku-nor.

**ampla** (ra, sf)—*[Colias croceus] ampla* Verity, 1919—048:87—Syntypes 1♂, 4♀♀ [Italy]: Isola di Sicilia: Palermo: San Martino: Monreale: 800 m: 18-28 V 1918: Querci [leg.]—Proposed for *Pontia daplidice* ('lapsus calami') and corrected to *Colias croceus* in 048:121.

**andromorphica** (ab)—*Leptidea sinapis sinapis andromorphica* Verity, 1911—010:343—[France]: Corsica.

**antehyale** (sr, sf)—*Colias hyale hyale antehyale* Verity, 1947—117:264—Syntypes 2♂♂ [Italy: Alto Adige]: Lago Maggiore: Intra: 200 m: 28 IV-4 V [19]27:

[Verity leg.].

**antemanni** (sf)—*Pieris manni manni antemanni* Verity, 1937—101:12—Syntypes 6♂♂, 5♀♀ [Yugoslavia: Dalmatia]: Spalato: 17-25 V 1910: Grund leg.

**antetodaroana** (sf)—*Pieris manni todaroana antetodaroana* Verity, 1937—106: 40—Syntypes 7♂♂, 5♀♀ [Italy: Sicily]: Palermo: IV 1912: Costantini [leg.]; Palermo: Trabia: V-VI 1930.

**anteubercalida** (sf)—*Colias hyale calida ubercalida anteubercalida* Verity, 1947—17:258—Syntype ♂ [France]: A[lpes]-M[aritimes]: [Nizzardo]: Le Bar-s[ur]-Loup: 12 V [19]36: Gazel [leg.].

**anteveragra** (sf)—*Pieris manni veragra anteveragra* Verity, 1935—094:44—Syntypes 5♂♂ [Switzerland: Wallis]: Martigny: 20 & 28 VI 1933: Verity [leg.].

**anticopupilata** (if)—*Colias phicomone anticopupilata* Verity, 1947—117:269—Syntype ♂ [N. Italy: Dolomiti]: Val Pesarina: M. Talm: 1700 m: 14 VII [19]36: Rocci leg.

**APHRODITE** (ssp)—*Colias eogene aphrodite* Verity, 1909—010:248—[W. China]: E. Turkestan: Aksou.

**apicenundata** (if)—*Pieris napi vulgaris apicenundata* Verity, 1916—033:79—S. England: [Westcliff-on-Sea: Conquest leg.]—Syntype(s) destroyed by museum pests.

**appendiculata** (if)—*Colias hyale hyale appendiculata* Verity, 1947—117:260—Syntype ♂ [Italy: Alto Adige]: Lago Maggiore: Intra: 200 m: 28 IV-4 V [19]27: [Verity leg.].

**arctica** (ra)—*Pieris napi frigida arctica* Verity, 1911—020:334—Scandinavia: [N. Norway]: Finmark—Müller & Kautz (1939): *Pieris arctica* [nec Verity], species.

**arctica** (ra)—*Colias palaeno europome arctica* Verity, 1908—010:216—Syntype ♂ [U.S.S.R.: N.E.] Sibiria: Wittim: 10-22 VII [18]88: Coll. Fruhstorfer.

**atomosa** (ra)—*Pieris crataegi atomosa* Verity, 1907—010:120—Syntypes 1♂, 1♀ [W. China: Szechwan]: Ta-Tsien-Lou: 1902: Chasseurs indigenes du P. Dejean.

**aurantiaca** (ab)—*Euchloe belia simplonia aurantiaca* Verity, 1908—010:179—France: Basses Alpes.

**aurantiaca** (fm)—*Colias ershoffi aurantiaca* Verity, 1909—010:253—W. Thian-shan: Ili River.

**aurantiacoflava** (fm)—*Colias erschoffi aurantiacoflava* Verity, 1909—010:253—Thian-shan.

**australis** (ra)—*Colias hyale hyale australis* Verity, 1911—010:347—Spain: Andalusia—Hemming & Berger (1950): *Colias australis* [nec Verity], species; junior subjective synonym of *Colias alfacariensis* Berger, 1948 (Kudrna 1982).

**australis** (ra)—*Pieris melete melete australis* Verity, 1911—010:331—Syntypes 2♂♂, 1♀ [China]: Haut Yunnan: Tali.

**BELIOIDES** (ssp)—*Euchloe belia belioides* Verity, 1911—010:339—U.S.A.: Arizona; U.S.A.: Montana: S. Ignatius.

**bimaculata** (if)—*Pieris rapae bimaculata* Verity, 1917—034:181—[Italy]: Isola d'Elba.

**bivittata** (nomen nudum)—*Leptidea sinapis bivittata* Verity, 1916—033:98—Name for seasonal form published without description, definition or indication.

**bivittata** (sf)—*Leptidea sinapis bivittata* Verity, 1917—034:182—Syntypes 3♂♂, 1♀ Italia centrale: Toscana: Firenze: Colline di Firenze: Fontebuona [di Vaglia]: Mt. Conca: 2 VII 1914: Querci [leg.].

**britannica** (ra)—*Pieris napi napi bitannica* Verity, 1911—010:332—Syntypes 3♂♂, 4♀♀ Scozia [= Scotland]: Costa sett. [= northern coast]: VII [19]08—Müller & Kautz (1939): *Pieris napi britannica* [nec Verity], subspecies.

**britannica** (ra)—*Euchloe cardamines cardamines britannica* Verity, 1908—010: 190—Syntypes 6♂♂ [England]: Northants: Barnwell Wood, Ashton Wold: 23 V 1875, 15 VI 1873; Chattenden: [illegible]: 17 V 1875; Sussex: Ashdown Forest: 24 V 1874; [all] Conquest leg.—Rest of type-series destroyed by museum pests.

**brunnea** (fm)—*Pieris largeteaui brunnea* Verity, 1907—010:124—[W. China]: W. Szechwan: Tatongkiao.

**brunneoviridis** (ab)—*Colias eogene eogene brunneoviridis* Verity, 1909—010: 245—[U.S.S.R.]: Alai.

**bryonapaeae** (sf, ra)—*Pieris napi bryonapaeae* Verity, 1926—058:173—Syntypes 7♂♂, 5♀♀ [N. Italy: Alpi Pennine]: Vanzone: 5-31 VII [19]24: [Verity leg.].

**bryoniaelutea** (if)—*Pieris napi bryoniae bryoniaelutea* Verity, 1947—117:202—N. Italy: Alpi Carniche: Sappada: 1600 m.

**bryonides** (fm)—*Pieris napi bryoniae bryonides* Verity, 1911—010:332—Syntypes 10♂♂, 5♀♀ [N. Italy: Alpi Marittime: Terme di] Valdieri: 9 VIII [19]09, 20 VIII 1909—Date of publication [31] X 1911.

**byronides** (sf)—*Pieris napi bryoniae bryonides* Turati & Verity, 1911—015:199—Junior objective homonyn and synonym of *Pieris napi bryoniae bryonides* Verity, 1911; date of publication 31 XII 1911.

**bryoniella** (if, ra)—*Pieris napi bryoniella* Verity, 1926—058:172—[N. Italy: Alpi Cozie]: Clavieres—Name proposed for a small form of male, characteristic for race ('racial').

**caerulea** (ab)—*Colias edusa caerulea* Verity, 1904—004:54—Italy: Toscana: Alpi Apuane: Mt. Matanna: 4000 ft.: VIII 1902.

**caerulescens** (if)—*Gonepteryx cleopatra europaeus caerulescens* Verity, 1919—042:87—Syntypes 1♂, 1♀ Italia centrale: Firenze: Fiesole: 18 VII; Firenze: Pian [di] Mugnone: 18 VIII 1917.

**calida** (sf)—*Colias hyale calida* Verity, 1916—033:99—Syntypes 1♂, 1♀ [Italy: Toscana: Firenze: Arezo]: Camaldoli: Val d'Arno superiore: [800-1000 m]: VIII [1]900: [Verity leg.]—Later treated by Verity (1947) as race (117:265).

**cana** (if)—*Leptosia sinapis nigrescens cana* Verity, 1922—042:92—syntypes 1♂, 2♀♀ Italia centrale: Toscana: Firenze: Pian di Mugnone: 200 m: 1 V 1917, 17 IV 1919: Querci [leg.]—Status of syntypes is questionable.

**cardaminesmontivaga** (ra)—*Anthocharis cardamines montivaga cardaminesmontivaga* Verity, 1934 [nec Linnaeus & Turati]—094:39—Switzerland: Martigny: Bex—Name for transitional local race.

**carnea** (ab)—*Pieris napi napi carnea* Verity, 1908—010:149—England: Lewis Island.

**castellana** (nomen nudum)—*Euchloe tagis bellezina castellana* Verity, 1911—010:339—Name for race published without description, definition or indication—

Manley & Allcard (1970) treated *Euchloe tagis castellana* as subspecies [nec Verity] but as they failed to provide description, definition or indication the taxon remains nomen nudum.

**caucasica** (ra)—*Pieris napi bryoniae caucasica* Verity, 1908—010:144—Syntypes 4♂♂, 3♀♀ [U.S.S.R.]: Caucasus sept. occ.: Kub[an] Geb[iet]: 12 IV [19]03, 1-6 VI [19]02: Coll. Bartel—Müller & Kautz (1939): *Pieris napi caucasica* [nec Verity], subspecies.

**cellulalunata** (if)—*Pieris ergane cellulalunata* Verity, 1947—117:215—Syntype ♀ [Italy]: Abruzzi: Sirente: Monterotondo: 1500 m: VIII [19]41.

***centralasiae** (ra)—*Pieris crataegi centralasiae* Verity, 1911—010:325—[N. China]: Boro-koro Mts.: Defile de Atchal.

**chinensis** (ra)—*Gonepteryx rhamni nepalensis chinensis* Verity, 1909—010:284—Syntype ♀ China: [Szechwan]: Kiug-Kiang-pou, further material in coll. Oberthür in BM(NH)—Nekrutenko (1968): *Gonepteryx rhamni chinensis* [nec Verity], subspecies. Kudrna (1975) sunk *chinensis* as junior subjective synonym of *Gonepteryx carnipennis* Butler, 1885.

**chitralensis** (ra)—*Colias alpherakyi roschana chitralensis* Verity, 1911—010: 349—[Pakistan]: Chitral: Lake Shandur: 3600 m.

**chrysohyaleoides** (ab)—*Colias erate chrysohyaleoides* verity, 1908—010:219—Persia: Kouldser.

**chrysothemeformis** (if)—*Colias croceus chrysothemeformis* Verity, 1919—042: 87—Syntype (Holotype?) ♂ [Italy]: Firenze: Pian di Mugnone: 11 IV 1919: Verity [leg.]—Same specimen later named *regressa*.

**chrysothemides** (fm)—*Colias myrmidone chrysotheides* Verity, 1911—010:358—Greece.

**chrysothemoides** (fm)—*Colias erate chrysothemoides* Verity, 1908—010:219—[U.S.S.R.]: Russia: Poltava.

**chrysothemoides** (fm)—*Colias hecla hecla chrysothemoides* Verity, 1911—010: 356—[N. America]: Territore de Barren.

**chryseis** (ra)—*Colias melinos chryseis* Verity, 1911—010:354—[U.S.S.R.: Far East]: Amur.

**cisalpina** (sr, sf)—*Pieris mannii pedemontana cisalpina* Verity, 1947—117:229—Syntypes 9♂♂, 3♀♀ [Italy: Alessandria: Nuove Terme di] Acqui: 4-10 VIII [19]12: [Verity leg.].

**commaculata** (ab)—*Euchloe cardamines commaculata* Verity, 1908—010:191—England.

**confluens** (fm)—*Pieris manni confluens* Verity, 1911—010:336—[France]: Pyrenees-Orientales.

**conjugata** (fm)—*Pieris rapae conjugata* Verity, 1911—010:335—Holotype ♀ [China]: Tsintau: [Coll.] Fruhstorfer.

**conjuncta** (fm)—*Colias erate conjuncta* Verity, 1908—010:219.

**corsica** (ra)—*Leptidea sinapis sinapis corsica* Verity, 1911—010:343—[France]: Corsica.

***crataegiaugusta** (ra)—*Aporia crataegi crataegiaugusta* Verity, 1937 [nec Linnaeus & Turati]—101:13—Greece: Mt. Olympus: 300 m: V-VI.

**cremonae** (ab)—*Colias croceus cremonae* Verity, 1911 [nec Bang-Haas]—010: 358—Syria.

**creta** (if, sf, ra)—*Pieris manni creta* Verity, 1919—042:88—Syntypes 4♂♂, 5♀♀ [Italy: Firenze]: Fiesole: Monte Fanna: 17-20 VI 1917; all remounted and relabelled—Name for individual peculiar to seasonal form and characteristic for 'race which produces it.'

**cypria** (ra)—*Pieris brassicae brassicae cypria* Verity, 1908—010:163—Cyprus: Larnaca.

**dalmatica** (ra)—*Gonepteryx cleopatra dalmatica* Verity, 1911—010:286—Syntypes 1♂(?), 2♀♀ [Yugoslavia]: Dalmatia.

**deckerti** (ra)—*Colias melinos deckerti* Verity, 1909—010:236—[U.S.S.R.]: S.E. Sibiria: Mt. Apfel.

**decolorata** (ab)—*Zegris fausti decolorata* Verity, 1908—010:170—[U.S.S.R.]: Krasnowodsk.

**deleta** (ab)—*Euchloe belia occidentalis deleta* Verity, 1908—010:179—France: Basses-Alpes.

**denticulata** (fm)—*Colias thisoa thisoa denticulata* Verity, 1909—010:252—Thianshan: Korla.

**deserticola** (ra)—*Leptidea sinapis sinapis deserticola* Verity, 1908—010:202—Syntypes(?) 2♂♂ N. Syria: Shar Deresy: [ex] Coll. Leech or specimens from Beyrut(?) which were not found—Ellison & Wiltshire 91939): *Leptidea sinapis deserticola* [nec Verity], subspecies.

**deserticola** (ra)—*Colias aurorina aurorina deserticola* Verity, 1909—010:258—[U.S.S.R.]: Armenia: mountains.

**deserticola** (ra)—*Colias croceus deserticola* Verity, 1909—010:268—Algeria: deserts.

**detersa** (ra)—*Euchloe bieti detersa* Verity, 1908—010:188—Syntype 1♀ China cent. occ.: Amdo.

**detersa** (ab)—*Euchloe cardamines detersa* Verity, 1908—010:191.

**detersa** (fm)—*Pieris ergane detersa* Verity, 1908—010:153—[Turkey]: Taurus: Barud dagh—Larsen (1974): *Pieris ergane detersa* [nec Verity], subspecies.

**diffusa** (ab)—*Colias erate diffusa* Verity, 1908—010:219—Persia: Kouldser.

**diniensis** (if)—*Leptidea lathyri diniensis* Verity, 1947—117:117.

**edusoides** (fm)—*Colias erate edusoides* Verity, 1908—010:219—[U.S.S.R.]: Russia: Poltava.

**eluta** (ab)—*Pieris daplidice eluta* Verity, 1911—010:327—Holotype(?) ♀ [Italy]: Elba: Marciana: 14 VII [19]08: [Verity leg.].

**emibryoniae** (if)—*Pieris napi emibryoniae* Verity, 1922—042:128.

**emicana** (ab)—*Pieris manni emicana* Verity, 1917—034:181—Italy: [?].

**emiorientalis** (ra)—*Euchloe belia creusa emiorientalis* Verity, 1911—010:338—[U.S.S.R.]: Altai: Ongodai: 900-1500 m; Kamtchatka.

**emisinapis** (ra)—*Leptidea amurensis emisinapis* Verity, 1911—010:345—Syntypes 1♂, 1♀ [U.S.S.R.]: Irkutsk.

**emivittata** (fm)—*Colias staudingeri emivittata* Verity, 1909—010:241—[China]: E. Turkestan: Aksu.

**eogenei** (ra)—*Colias eogene arida eogenei* Verity, 1909 [nec Deckert]—010:246—[China]: E. Turkestan: Aksu.

**erysimi** (if)—*Leptidea lathyri erysimi* Verity, 1947—117:117.

**EUORIENTIS** (ssp)—*Pieris napi euorientis* Verity, 1908—010:147—Syntypes 3♂♂ [U.S.S.R.]: Sajan: Muorku; Ostsajan.

***europaeus** (ra)—*Gonepteryx cleopatra europaeus* Verity, 1913—023:180—Syntypes 2♂♂, 1♀ [Italy: Toscana]: Firenze: 5 V [19]08, 27 VI [19]08, 16 III [18]99: [Verity leg.]—Nekrutenko (1968): *Gonepteryx cleopatra europaeus* [nec Verity], subspecies. Kudrna (1975) sunk *europaeus* as junior subjective synonym of *G. cleopatra italica* (Gerhardt, 1882). *G. cleopatra* (Linnaeus, 1767) is probably best treated as monotypic species with pseudopolytypic variation.

**evanescens** (fm)—*Pieris ergane evanescens* Verity, 1908—010:153—Greece.

**evanescens** (ra)—*Colias cocandica grumi evanescens* Verity, 1909—010:233—[China]: Lob-nor.

**exigua** (sf)—*Pieris ergane exigua* Verity, 1923—052:18—Syntypes 1♂, 7♀♀ Italia centrale: Marche: [Mti Sibillini]: Alto Valle de Fergano: 1400 m: 20-21 VIII 1921: Querci [leg.]—Name for seasonal form of autumn generation (gen. 3), indirectly applied to race and published as synonym of *ergane*.

**exigua** (nomen nudum)—*Pieris egane exigua* Verity, 1923—052:18—Name proposed for race and published without description, definition or indication.

**expansa** (if, ra)—*Pontia daplidice expansa* Verity, 1919—042:87—Syntypes 5♂♂, 4♀♀ [Italy: Firenze]: Pian di Mugnone: [200 m]: 16 VI-1 VII 1917: [Querci leg.]; all remounted and relabelled—Name for large individual form applied to 'the race that produces it.'

**extraordinaria** (sf)—*Euchloe ausonia romana extraordinaria* Verity, 1947—117:170—Italy: Caserta: Setteptrati: 800 m: 21 X [????].

**flava** (ab)—*Colias chrysotheme flava* Verity, 1908—010:pl.XLIX, fig. 41—Syntype ♀ 11 IV [19]06—Same aberration named *flavescens* in 010:273.

**flavescens** (fm)—*Colias chrysotheme chrysotheme flavescens* Verity, 1909—010:273—Syntype ♀ 11 IV [19]06—Same individual form named *flava* in 010:pl. XLIX, fig.41.

**flavescens** (if)—*Leptidea lathyri flavescens* Verity, 1947—117:117.

**flavointerjecta** (if)—*Pieris napi flavointerjecta* Verity, 1926—058:172—Syntype ♀ [Italy]: Südtirol: 1916: [Wagner leg.].

**flavolimbata** (fm)—*Colias staudingeri flavolimbata* Verity, 1909—010:241—[China]: E. Turkestan: Aksu.

**flavopicta** (nomen nudum)—*Pieris chloridice chloridice flavopicta* Verity, 1911—010:328—Nomen collectivum for individual form given rank of race and published without description, definition or indication.

**flavosatura** (if, ra)—*Pieris napi flavosatura* Verity, 1926—058:172—Syntypes 3♀♀ [Austria]: Tirol: Hintertux: 1920—Name for individual form of female applied also to race.

**flavosignata** (fm)—*Colias hyale poliographus flavosignata* Verity, 1909—010:224—China: Kokunoor.

**fragilis** (ra, sf)—*Leptidea duponcheli fragilis* Verity, 1937—101:10—[Greece]: Thesaloniki: V—Name for seasonal form and local race also applicable to specimens from Turkey: Ak-Chehir.

**fountaineae** (ra)—*Colias aurorina heldreichi fountaineae* Verity, 1911—010:357—Greece: Mt. Chelmos.

**fountaineae** (ab)—*Pieris napi napi fountaineae* Verity, 1911—010:331—[Yugoslavia]: Dalmatia: Cattaro.

**fulgida** (fm)—*Colias cocandica cocandica fulgida* Verity, 1911—010:354—Ladakh.

**gallica** (ra)—*Euchloe tagis bellezina gallica* Verity, 1908 [nec Oberthür]—010:183—Hautes Alpes.

**gigantea** (ra)—*Colias erate gigantea* Verity, 1911—010:347—E. Pamir: Aksu.

**graeca** (ra)—*Euchloe belia belia graeca* Verity, 1908 [nec Staudinger]—010:175—Greece: Mt. Parnass; [Yugoslavia]: Dalmatia.

**graeca** (ra)—*Colias chrysotheme chrysotheme graeca* Verity, 1911—010:359—Greece.

**graeca** (fm)—*Euchloe cardamines cardamines turritis graeca* Verity, 1911—010:341—Greece.

**granatae** (ra)—*Euchloe tagis tagis granatae* Verity, 1911—010:339—[Spain]: Andalusia: Granada.

**grandis** (if)—*Leptosia sinapis diniensis grandis* Verity, 1922—042:91—Syntypes 10♂♂, 3♀♀ [Italy: Firenze]: Pian di Mugnone: 16-27 VI 1915; all remounted and relabelled.

**grandisbivittata** (if)—*Leptosia sinapis grandisbivittata* Verity, 1922—042:91.

**griseoviridis** (fm)—*Colias aurorina heldreichi griseoviridis* Verity, 1909—010: 260—Greece.

**grisescens** (ab)—*Euchloe belia simplonia oberthueri grisescens* Verity, 1908—[nec Oberthür]—010:179—France: Hautes-Pyrenees: Gedre.

**gyantsensis** (ra)—*Pieris dubernardi chumbiensis gyantsensis* Verity, 1911—010: 329—Gyantsee: 3900 m.

**gynomorpha** (ab)—*Colias phicomone gynomorpha* Verity, 1911—010:353—Switzerland: Engadin.

**helicoides** (fm)—*Colias chrysotheme chrysotheme helicoides* Verity, 1911—010: 358—Austria.

**hemiandegava** (sr, if)—*Pieris mannii gallia hemiandegava* Verity, 1947—010:228—Syntype ♀ [France: Alpes-Maritimes]: Therenc: [1370m]: 2 VIII [19]34: [Verity leg.].

**hinducucica** (ra)—*Pieris callidice hinducucica* Verity, 1911—010:326—Hindukush.

**hinducucica** (ra)—*Colias cocandica hinducucica* Verity, 1911—010:353—Hindukush.

**hyalides** (fm)—*Colias phicomone hyalides* Verity, 1911—010:353—Baviere merid.: Saitan.

**hybrida** (ab)—*Colias aurorina libanotica hybrida* Verity, 1909—010:259—Persia—Not listed in systematic index (010:XXXIX).

**immaculata** (fm)—*Pieris ergane immaculata* Verity, 1908—010:153—Greece.

**immaculata** (ra)—*Colias thisoa immaculata* Verity, 1909—010:252—[U.S.S.R.]: Issyk-Kul.

**impunctata** (fm)—*Colias phicomone impunctata* Verity, 1909—010:230—Spain: Asturia: Picos d'Europa: 2000m.

**impunctata** (fm)—*Colias myrmidone impunctata* Verity, 1909—010:264—Bohemia.

**infracaerulescens** (if)—*Colias croceus infracaerulescens* Verity, 1947—117: 280—Holotype(?) ♀ [Italy]: Toscana: [Firenze]: Colline di Firenze: 200 m: 14 X 1921: Querci [leg.]; 'olotipo': *infracaerulescens*.

**infralutea** (if)—*Colias croceus infralutea* Verity, 1947—117:280.

**infraochreata** (if)—*Aporia crataegi infraochreata* Verity, 1919—042:88—Syntype ♀ [Italy: Alpi Marittime: Terme di Valdieri]; type: *infraochreata*.

**infraviridis** (if)—*Colias croceus infraviridis* Verity, 1947—117:280.

**insularis** (ra)—*Gonepteryx cleopatra insularis* Verity, 1911—010:286—Syntype(?) 1♂ [Italy]: Sardegna: Cagliari—Nekrutenko (1968): *Gonepteryx cleopatra insularis* [nec Verity], subspecies. Kudrna (1975) sunk *insularis* as junior subjective synonym of *G. cleopatra italica* (Gerhardt, 1882).

**integra** (fm)—*Colias cocandica integra* Verity, 1911—010:353—Hindukush: Beik.

**intermedia** (nomen nudum)—*Gonepteryx rhamni intermedia* Verity, 1916—031: 51—Name published without description, definition or indication.

**japona** (ra)—*Leptidea amurensis japona* Verity, 1911—010:345—Holotype ♂ [Japan: Yokohama].

**jurassica** (ra)—*Colias palaeno europome jurassica* Verity, 1908—010:216—Jura.

**kachgarica** (ra)—*Colias hyale poliographus kachgarica* Verity, 1911—010:348—Thibet occ.: Kachgar.

**lanceolata** (if)—*Colias phicomone lanceolata* Verity, 1947—117:270—Syntype ♂ [Italy: Dolomiti]: Alpi Agordine: Falcade: P[onte] de la Schita: 2000 m: 27 VII 1937: Rocca [leg.].

***lathyricana** (ra)—*Leptidea sinapis lathyricana* Verity, 1947 [nec Hübner & Verity]—117:131—N. Italy: Alpi Carniche: Sappada: 20 VI-30 VII [????]—Name for transitional race composed of two forms and originally published hyphenated.

**lathyrides** (ra)—*Leptidea sinapis sinapis lathyrides* Verity, 1911—010:344—Syntypes 2♂♂ [U.S.S.R.]: Amur.

**leucodiciformis** (if)—*Synchloe callidice leucodiciformis* Verity, 1947—117:185—Italy: Alpi Pennine: Monte Cervino: Val Tornenza: 16 VIII [????].

**limbata** (if)—*Anthocaris damone limbata* Verity, 1947—117:142—Greece.

**linnaei** (sf)—*Pieris napi linnaei* Verity, 1922—042:134—Syntypes 8♂♂, 6♀♀ [C.] Sweden: Norrweken: VI, 25 VII, VIII [19]21.

**lorkovici** (hy)—*Pieris lorkovici* Verity, 1947—117:222—Name for hybrid *P. rapae* ♂ x *P. mannii* ♀.

**lucillides** (fm)—*Euchloe charlonia lucilla lucillides* Verity, 1911—010:341—[W. Pakistan]: Campbellpore.

**luctifica** (ab)—*Zegris eupheme luctifica* Verity, 1908—010:169—[S. Spain]: Andalusia: Rivas.

**magna** (if, sf)—*Leptosia sinapis bivittata magna* Verity, 1922—042:91—Syntypes 3♂♂, 1♀ [Italy: Alpi Marittime: Terme di] Valdieri: [1375 m]: 25 & 27 VII [19]09, 15 & 25 VII [19]11: [Verity leg.].

**magnadiniensis** (if)—*Leptosia sinapis magnadiniensis* Verity, 1922—042:91.

**magnomaculata** (ab)—*Pieris callidice magnomaculata* Verity, 1911—010:326—Hindukush: Kounjout: Hunza.

**major** (ra)—*Gonepteryx aspasia aspasia major* Verity, 1909—010:280—[China]: Szechwan—Nekrutenko (1968): *Gonepteryx rhamni major* [nec Verity], subspecies; Kudrna(1975): *Gonepteryx maxima major* [nec Verity], subspecies.

**major** (if)—*Synchloe callidice major* Verity, 1947—117:185.

**major** (if)—*Euchloe ausonia major* Verity, 1947—117:159—[Italy]: Genova: Quezzi: 12 IV [????].

**major** (if)—*Pieris brassicae brassicae major* Verity, 1947—117:242—[Italy: Milano]: Soria: 16 VI [????].

**majorides** (ra)—*Leptidea sinapis sinapis majorides* Verity, 1911—010:344—[U.S.S.R.: Ukraine]: Kiev.

**majorina** (sr, if)—*Gonepteryx cleopatra europaeus majorina* Verity, 1947—117:296—Syntype ♀ [Italy: Toscana]: Spezia: Lerici: 19 VIII [19]13: [Verity leg.].

**mannides** (hy, ab)—*Pieris rapae mannides* Verity, 1911—010:XXIX, pl. XXXII, ifg. 51—[Italy: Toscana]: Vallombrosa: 1000 m.

**mariformis** (if)—*Pontia daplidice mariformis* Verity, 1947—117:178—[Italy]: Firenze: Verity [leg.].

**mascula** (fm)—*Gonepteryx rhamni amintha mascula* Verity, 1911—010:285—[W. China]: Szechwan: Moupin.

**matutiacramerigenuensis** (sr)—*Euchloe ausonia crameri matutiacramerigenuensis* Verity, 1947—117:168—Syntypes 2♂♂, 1♀ [Italy]: Genova, [Genova]: Quezzi: 12-27 IV [1]919: Rocci [leg.].

**maura** (ra)—*Pieris napi napi maura* Verity, 1911—010:332—Syntypes 5♂♂, 1♀ Algeria: Blidah: V 1904: M. E. F[ountaine leg.], all deposited in Castle Museum, Norwich (England)—Warren (1970): *Pieris maura* [nec Verity], species.

**mauritanica** (ra)—*Pieris rapae mauritanica* Verity, 1908—010:155—Algeria; Morocco: Tangier.

**maxima** (ra)—*Euchloe belia belia maxima* Verity, 1908—117:177—Syntypes 2♂♂ [U.S.S.R.]: Krim.

**maxima** (if)—*Pieris rapae rapae secunda maxima* Verity, 1947—117:233—[Italy: Firenze]: Pian di Mugnone: 11, 12, 30 VI [????].

**mediodilata** (if)—*Pontia daplidice mediodilata* Verity, 1947—117:180—Holotype ♀ [Italy: Elba]: Spiaggia: Magazzini: 20 VII [19]08: [Verity leg.].

**melanina** (ab)—*Colias hyale melanina* Verity, 1909—010:223.

**melanitica** (ab)—*Colias croceus melanitica* Verity, 1909—010:270—S. Italy: Sorrente.

**melanochroa** (fm)—*Pieris goutellei melanochroma* Verity, 1908—010:126—[China]: W. Szechwan: Tsekou.

**melanoinspersa** (ab)—*Leptidea sinapis sinapis melanoinspersa* Verity, 1911—010:344—Turkestan.

**melinoides** (if)—*Colias phicomone melinoides* Verity, 1926—058:171—Syntype ♂ [locality unspecified]; type: *melinoides*.

**meridionalis** (ra)—*Euchloe cardamines cardamines meridionalis* Verity, 1908—010:190—Italy: Firenze.

**meridionalis** (ra)—*Pieris crataegi meridionalis* Verity, 1911—010:324—Syria: Shar Deresy; Asia Minor; S. Europe—Manley & Allcard (1970): *Aporia crataegi meridionalis* [nec Verity], subspecies.

**meridionalissubnapaeae** (ra)—*Pieris napi meridionalissubnapaeae* Verity, 1947—117:208—[Italy]: Torino, Venezia Giulia—Name for transitional 'race' proposed in hypenated form.

**metabryoniae** (sf)—*Pieris napi metabryoniae* Verity, 1926—058:173—Syntypes 6♂♂, 11♀♀ [Italy]: Alpi Pennine: Vanzone: 17-19 VIII [19]24, 7-23 VIII [19]25: [Verity leg.].

**microbutleri** (sf)—*Euchloe ausonia crameri microbutleri* Verity, 1947—117:168—Syntype ♂ [Italy]: Modena: M. Gibbio: VI [19]06: Costantini [leg.]; at least 1♀ syntype destroyed by museum pests.

**microcrameri** (sr, sf)—*Euchloe ausonia crameri microcrameri* Verity, 1947—117:168—Syntypes 2♂♂, 1♀ [Italy]: Modena; Modena: Altareto: V [1]903.

**micromeridionalis** (sr, sf)—*Pieris napi micromeridionalis* Verity, 1922—042: 138—[Italy]: Forte dei Marmi, Vallombrosa, Piteglio, Appennino Pistoiese, Luca, Prato Fiorito, Bolognola—Name proposed for 'grade' in variation applicable to seasonal form and race.

***micromorsei** (ra)—*Leptidea morsei micromorsei* Verity, 1947—117:120—[U.S.S.R.]: Amur: Pochrofka.

**microsticta** (if)—*Pieris mannii microsticta* Verity, 1947—117:222—[Italy: Firenze]: Sesto Fiorentino: 18 VI [????].

**microvulgaris** (ra, sf)—*Pieris napi microvulgaris* Verity, 1927—064:173—[S. Spain]: Sierra Nevada: Aldaire: 1400 m; Velez del Marquesado: 1400 m; summer generation only.

**minima** (fm)—*Pieris manni minima* Verity, 1908—010:154—Italy: Firenze.

**minima** (fm)—*Pieris canidia minima* Verity, 1908—010:161—Thibet: Chapa.

**minor** (fm)—*Pieris crataegi minor* Verity, 1907 [nec Oberthür]—010:119—France: Pyrenees Orientales: Vernet-les-Bains.

**minor** (ra)—*Pieris melete melete minor* Verity, 1911—010:330—Amur, Korea.

**minor** (if)—*Euchloe ausonia minor* Verity, 1947—117:159—[Italy]: Liguria: San Remo.

**minuscula** (fm)—*Pieris daplidice minuscula* Verity, 1911—010:327—[U.S.S.R.]: Sarepta.

**monovittata** (nomen nudum)—*Leptosia sinapis monovittata* Verity, 1924—053: 111—Name for seasonal form published without description, definition or indication.

**montana** (ra)—*Pieris melete melete montana* Verity, 1908—010:141—Sikkim: Lachin Lachoong.

**montana** (ra)—*Euchloe belia belioides montana* Verity, 1911—010:339—[U.S.A.]: Colorado: Hall Valley: 3000 m.

**montana** (ra)—*Colias melinos montana* Verity, 1911—010:354—Altay: Tchuja Mts.: 1800-2400 m.

**MONTIVAGA** (ssp)—*Euchloe cardamines montivaga* Turati & Verity, 1912—020:232—Syntypes 4♂♂ [Italy: Alpi Marittime: Terme di] Valdieri: [1375 m]: 14-25 VII [19]11: Verity [leg.].

**morseides** (fm)—*Leptidea sinapis morsei morseides* Verity, 1911—010:244—Syntypes 3♂♂ Sajan: Tonkoun.

**narina** (ra)—*Pieris napi ochsenheimeri narina* Verity, 1908—010:145—[U.S.S.R.]: Turkestan: Naryn.

**nastoides** (fm)—*Colias cocandica cocandica nastoides* Verity, 1911—010:354—Transalai: Aram Koungai.

**neobryoniaeflavescens** (nomen nudum)—*Pieris napi neobryoniaeflavescens* Verity, 1947—Name for individual form published hyphenated without description, definition or indication.

**nigrans** (ab)—*Pieris napi napi nigrans* Verity, 1908—010:150—Germany: Schlesien.

**nigrans** (if)—*Pontia daplidice nigrans* Verity, 1947—117:178—Holotype(?) ♀ [Italy]: Abruzzi: Gran Sasso: 1300-1500 m: 27 VIII 1939: Romei [leg.]; 'olotipo': *nigrans*.

***nigrescens** (ra)—*Leptidea sinapis nigrescens* Verity, 1919—042:87—Syntypes 4♂♂ It[alia] centr[ale]: [Toscana]: Marina di Pisa: Antico greto dell'Arno: 26 V 1917: Verity [leg.].

**nigricans** (fm)—*Pieris davidis nigricans* Verity, 1908—010:137.

**nigrofasciata** (ab)—*Colias croceus nigrofasciata* Verity, 1909—010:269—[U.S.S.R.]: Russia: Sarepta.

**nigroinspersa** (fm)—*Pieris leucodice illumina nigroinspersa* Verity, 1911—010:326—[U.S.S.R.: C. Asia]: Hissar Mts.

**niphonica** (ra)—*Pieris rapae niphonica* Verity, 1908—010:156—Syntypes 1♂, 1♀ Asien: Japan.

**niphonica** (ra)—*Gonepteryx aspasia aspasia niphonica* Verity, 1909—010:280—Syntype ♂ Giappone [= Japan]: Fuzitama [= Fujiyama]: 16 VIII [1]902—Nekrutenko (1968): *Gonepteryx aspasia niphonica* [nec Verity], subspecies. Kudrna (1975): *G. aspasia niphonica* [nec Verity].

**nitida** (ra)—*Pontia daplidice nitida* Verity, 1908—010:132—Syntypes 2♂♂, 2♀♀ Asia Minor: Fanaraki; [Spain]: Andalusia: Malaga: Ribbe [leg.].

**niveata** (fm)—*Colias sifanica nebulosa niveata* Verity, 1909—010:228—[China]: Kukunoor.

**oberthueri** (ra)—*Euchloe belia simplonia oberthueri* Verity, 1908—010:179—France: Hautes-Pyrerees: Gedre, Cauterets—Manley & Allcard (1970): *Euchloe simplonia oberthueri* [nec Verity], subspecies.

**oberthueri** (ra)—*Colias phicomone oberthueri* Verity, 1909—010:231—France: Pyrenees: Vernet-les-Bains, Gedre—Manley & Allcard (1970): *Colias phicomone oberthueri* [nec Verity], subspecies.

**oberthuri** (fm)—*Pieris bieti oberthuri* Verity, 1907—010:120—[China]: W. Szechwan: Tatsienlu.

**obliterata** (fm)—*Colias palaeno europome obliterata* Verity, 1911—010:346—Switzerland.

**obscurata** (ab)—*Colias nastes nastes obscurata* Verity, 1911—010:355—[Canada]: Alberta: Lake Luise.

**obscurata** (if)—*Leptidea sinapis obscurata* Verity, 1917—034:182—[Italy: Isola d'Elba].

**obscurissima** 9fm)—*Colias aurora obscurissima* Verity, 1911—010:357—[U.S.S.R.]: Altai: Ongodai: 3000-5000 m.

**OCCIDENTALIS** (ssp)—*Euchloe belia occidentalis* Verity, 1908—010:175—Syntypes 3♂♂, 1♀ Francia centrale; Algeria: Tingrad; Verity (010: XXXI) listed distribution: southern and western Mediterranean, as race also in Syria and race *occidentalis* has distribution N. Italy, France, Spain.

**ochracea** (nomen nudum)—*Gonepteryx rhamni ochracea* Verity, 1919—042:48—Name for individual form published without description, definition or indication.

**ochreata** (if, sf)—*Pieris napi napeae ochreata* Verity, 1919—042:87.

**ochreata** (if)—*Gonepteryx cleopatra europaeus ochreata* Verity, 1919—042:87—Syntype 1♂ [Italy]: Firenze: VIII [19]07: [Verity leg.].

**octobris** (sf)—*Pontia daplidice octobris* Verity, 1923—052:17—Syntypes 3♂♂, 3♀♀ [Italy]: Toscana: Firenze: Colline di Firenze: 200 m: 15 X 1920, 10 X 1921: Querci [leg.].

**offusa** (ab)—*Colias aurorina libanotica offusa* Verity, 1909—010:259—N.E. Persia: Asterabad.

**orientalides** (ra)—*Euchloe belia belioides orientalides* Verity, 1908—010:182—Holotype(?) ♂ [U.S.A.]: California: Placer; data very poorly legible.

**orientalis** (ra)—*Euchloe cardamines cardamines orientalis* Verity, 1908—010:190—[U.S.S.R.]: Buchara: Nanking.

**palaenoides** (fm)—*Colias wiskotti wiskotti palaenoides* Verity, 1909—010:261—Turkomanie.

**parva** (fm)—*Pieris dubernardi dubernardi parva* Verity, 1908—010:136—[China]: W. Szechwan: Tsekou.

**passa** (ab)—*Colias croceus passa* Verity, 1909—010:269—Austria.

**passa** (ab)—*Colias phicomone passa* Verity, 1911—010:353—Switzerland: Engadin: Albula.

**PERSIS** (ssp)—*Pieris napi persis* Verity, 1922—042:140—Persia.

**phaiosoma** (sf)—*Pieris rapae phaiosoma* Verity, 1924—052:46—Syntypes 2♂♂, 1♀ [Italy]: Roma: Fiugi: 20-30 VIII [19]23: [Verity leg.].

**phicomonides** (fm)—*Colias nastes werdandi phicomonides* Verity, 1911—010:355—Norway: Quick Jock.

**postandegava** (nomen nudum)—*Pieris manni rossi postandegava* Verity, 1935—094:45—Name for seasonal form published without description, definition or indication.

**posteromaculata** (if)—*Pieris ergane posteromaculata* Verity, 1947—117:215—Holotype ♀ [Italy]: Roma: Fiuggi: 700 m: 25-28 VII [19]40: Verity [leg.].

**posticeochreata** (if)—*Pieris brassicae posticeochreata* Verity, 1919—042:88—Syntype ♀ [locality not known]; Type: *posticeochreata.*

**posticominuta** (if)—*Colias croceus posticominuta* Verity, 1947—117:285—Holotype ♂ [Italy]: Alpi Apuana: Monte Matanna: [1300 m]: VIII [1]903; 'olotipo': *posticominuta.*

**posticotersior** (if)—*Colias croceus posticotersior* Verity, 1947—Syntype ♀ [Italy]: Bergamo: Sombreno: 275 m: 20 VII [19]29: [Verity leg.].

**postmanni** (sf)—*Pieris manni postmanni* Verity, 1938—109:10—Syntypes 2♂♂ [Greece]: Macedonia: Salonika [= Thessaloniki]: [hills above town]: 1000 ft.: 13 XI 1936: Romei [leg.].

**postveraga** (sf)—*Pieris manni veraga postveraga* Verity, 1935—094:44—Syntypes 1♂, 1♀ [Switzerland: Wallis]: Martigny: 14 IX 1926: Coll. Fletcher.

**praenapaeae** (sf)—*Pieris napi septentrionalis praenapaeae* Verity, 1922—042: 137—Syntypes 5♂♂, 5♀♀ [France]: Eure: Pont-de-l'Arche: VII 1909, VII 1911, VII 1912, 26 VII 1915, VII 1916.

**praesemimaculata** (if)—*Pieris ergane praesemimaculata* Verity, 1947—117:217.

**pseudoausonides** (fm)—*Euchloe belia belioides pseudoausonides* Verity, 1911—010:339—U.S.A.: California.

**pseudobryoniae** (fm)—*Pieris napi frigida pseudobryoniae* Verity, 1908—010: 146—[U.S.A.]: Alaska: Nualto; Scandinavia: [N. Norway]: Finmark.

**pseudoduponcheli** (ra)—*Leptidea sinapis sinapis pseudoduponcheli* Verity, 1908—010:203—[France]: Pyrenees-Orientales: Vernet-les-Bains.

**pseudohippia** (ra)—*Pieris crataegi pseudohippia* Verity, 1911—010:325—Tibet.

**pseudohyale** (fm)—*Colias erschoffi pseudophyale* Verity, 1909—010:263.

**pseudoleracea** (ra)—*Pieris napi frigida pseudoleracea* Verity, 1908—010:146—Labrador.

**pseudomelete** (ra)—*Pieris napi euroerientis pseudomelete* Verity, 1908—010: 167—Holotype(?) ♀ [U.S.S.R.]: Ussuri.

**pseudonapi** (ra)—*Pieris melete melete pseudonapi* Verity, 1911—010:330—Japan: Yezo [= Hokkaido]: Ichikiri.

**pseudorapae** (ra)—*Pieris napi napi pseudorapae* Verity, 1908—010:144—Syntypes 3♂♂ Syria: Beyrouth; lectotype selected by Bowden & Riley (1967): *Pieris napi pseudorapae* [nec Verity], subspecies.

**pulchra** (ra)—*Colias berylla pulchra* Verity, 1911—010:351—Tibet: Lhasa: Khambajong: Gyantsee: 3900 m.

**pulverea** (fm)—*Pieris rapae pulverea* Verity, 1911—010:335—Gangi Hissar: Yarkaud.

***pulverulenta** (ra)—*Colias phicomone pulverulenta* Verity, 1926—058:170—Syntypes 7♂♂, 6♀♀ [Italy]: Alpi Cozie: Sestrieres: 2035 m: 8 VIII 1925: Verity [leg.].

**pulverulenta** (ab)—*Euchloe belia belia pulverulenta* Verity, 1908—010:178—France: Basses-Alpes: Heyeres.

**punctata** (fm)—*Pieris dubernardi dubernardi punctata* Verity, 1908—010:136.

**punctillata** (if)—*Gonepteryx cleopatra europaeus punctillata* Verity, 1947—117:295—Holotype(?) ♂ [Italy]: Firenze: Verity [leg.]; 'olotipo': *punctillata*.

**quadra** (fm)—*Euchloe belia occidentalis quadra* Verity, 1908—010:175—Spain: Madrid: El Pardo.

**regressa** (if)—*Colias croceus regressa* Verity, 1947—117:281—Syntype (Holotype?) ♂ [Italy]: Firenze: Pian di Mugnone: 11 IV 1916: Verity [leg.]—Same specimen named earlier *chrysothermeformis*.

**reniformis** (if)—*Euchloe ausonia reniformis* Verity, 1947—117:160—N. Italy: Pino Torinese: Podio: 410 m: 5 V [????].

**romanoides** (fm)—*Euchloe belia belia romanoides* Verity, 1908—010:177—Italy: Toscana: Firenze, Chianti.

**rondoui** (ab)—*Pieris callidice rondoui* Verity, 1908—010:131—Switzerland: Engadin.

**rondoui** (ab)—*Euchloe belia simplonia rondoui* Verity, 1908—010:180—France: Pyrenees: Gedre.

**roseosatura** (if)—*Colias croceus roseosatura* Verity, 1947—117:283—Syntype ♂ [Italy: Toscana: Lucca]: Forte dei Marmi: 5 X [1]903: [Verity leg.].

**rostagnoi** (fm)—*Pieris ergane rostagnoi* Verity, 1908—010:153—[Italy]: Abruzzi: Oricola.

**ROTHSCHILDI** (ssp)—*Pieris dubernardi rothschildi* Verity, 1911—010:329—N.E. China: Tsing-ling Mts.: Tai-pai-chan.

**rothschildi** (sf)—*Euchloe ausonia crameri rothschildi* Verity, 1923—050:171—Syntypes 1♂, 1♀ [Spain]: Andalusien: Granada: Mont[es]: Ribbe [leg.].

**rufa** (fm)—*Colias hyale hyale rufa* Verity, 1909—010:222—Turkestan.

**sajana** (ra)—*Euchloe cardamines cardamines sajana* Verity, 1908—010:190—Syntype ♂ Sajan.

**sajana** (ra)—*Pieris crataegi sajana* Verity, 1911—010:324—Syntypes 2♂♂, 2♀♀ Sajan: Tonkun, Tonkoun.

**secunda** (sf)—*Pieris rapae secunda* Verity, 1917—034:180—Italy: Elba(?).

**secunda** (nomen nudum)—*Gonepteryx cleopatra europaeus secunda* Verity, 1919—042:87—Name for seasonal form published without description, definition or indication.

**secunda** (sf)—*Gonepteryx rhamni transiens secunda* Verity, 1919—042:48.

**secundogenita** (sf)—*Pieris manni secundogenita* Verity, 1923—052:19—[Italy: Toscana: Lucca]: Forte dei Marmi(?).

**septembrina** (sf)—*Pieris manni septembrina* Verity, 1923—052:19—Syntypes 8♂♂, 12♀♀ [Italy: Firenze]: Pian di Mugnone: 200 m: 10-29 IX 1917; all remounted and relabelled.

***septentrionalis** (ra)—*Pieris napi septentrionalis* Verity, 1916—033:79—Syntypes 8♂♂, 2♀♀ S. England: Westcliff-on-sea: Conquest [leg.].

**sibirica** (ra)—*Pieris crataegi sibirica* Verity, 1911—010:324—Syntypes 15♂♂, 2♀♀ [U.S.S.R.]: Sibiria: Tomsk.

**sieversoides** (fm)—*Colias hyale hyale sieversoides* Verity, 1909—010:221—Germany: Württemberg.

**stauderi** (sf, ra)—*Pieris napi stauderi* Verity, 1922—042:139—Italy: Casserta: Mainarde.

**stefanellii** (fm)—*Pieris ergane stefanellii* Verity, 1908—010:153—Syntypes 13♂♂ Greece: Attica (8♂♂); [Italy: Abruzzi]: Oricola: 2 VIII [1]906, 25 VIII [19]09, 29 VIII [19]09, 25 IX [19]09: Verity [leg.]; status of syntypes(?) from Greece uncertain.

**subalbidice** (sf)—*Pontia daplidice subalbidice* Verity, 1923—052:17—Syntypes 2♀ Italia centrale: Toscana: Lucca: Forte dei Marmi: 2 m: 1-15 VIII 1917: Verity [leg.].

**subnapaeae** (sf, ra)—*Pieris napi subnapaeae* Verity, 1922—042:137—Syntypes

1♂, 2♀♀ [France: Oise]: Compiegne: 19 VII 1912—Name proposed for 'grade' in variation.

**sufflava** (if)—*Colias hyale sufflava* Verity, 1947—117:262.

**suffusa** (fm)—*Pieris napi bryoniae suffusa* Verity, 1908—010:143—[U.S.S.R.]: Trascaucasia: Jelizavetopol.

**sulphurea** (ab)—*Euchloe belia occidentalis sulphurea* Verity, 1908—010:178—France: Villenueve de Blaye.

**syra** (ra)—*Pieris krueperi syra* Verity, 1911—010:336—Syria: Shar Deresy.

**syra** (ra)—*Euchloe damone syra* Verity, 1911—010:342—Syntypes(?) 1♂, 1♀ Syria: [Ain Zahalta]—Larsen (1974): *Anthocharis damone syra* [nec Verity], subspecies.

**taipachnana** (ra)—*Euchloe cardamines cardamines taipachnana* Verity, 1911—010:341—China: Tsing-ling Mts.: Tai-pai-chan.

**tarda** (if)—*Pieris napi meridionalis tarda* Verity, 1922—042:139.

**tenuemaculosa** (if)—*Pieris napi meridionalis tenuemaculosa* Verity, 1922—042:139—[Italy]: Firenze.

**tertia** (sf)—*Pieris rapae tertia* Verity, 1917—034:180—[Italy]: Elba(?).

**tertia** (sf)—*Gonepteryx rhamni transiens tertia* Verity, 1919—042:48.

**tertia** (nomen nudum)—*Gonepteryx cleopatra europaeus tertia* Verity, 1919—042:87—Name for seasonal form published without description, definition or indication.

**tertia** (sf)—*Pieris brassicae tertia* Verity, 1919—042:88—Syntypes 5♂♂, 1♀ Italia centrale: Firenze: Pian di Mugnone: 200 m: 12 IX-10 X 1917: Querci [leg.].

**thibetana** (ra)—*Pieris davidis thibethana* Verity, 1908—010:137—[China]: Tibet: Kukunoor, Amdo.

**transiens** (fm)—*Pieris melete melete transiens* Verity, 1908—010:138—Amur, Manchuria: Is. Skold.

**transiens** (ra)—*Euchloe belia simplonia transiens* Verity, 1908—010:180—Syntype ♂ [U.S.S.R.]: Ferghana: Alai Thal.

**TRANSIENS** (ssp)—*Gonepteryx rhamni transiens* Verity, 1913—023:180—Syntype 1♂, 2♀♀ [Italy: Toscana]: Firenze: [illegible]: 13 II [1]902, 25 III [19]03, 14 IV [19]04: [Verity leg.]—Kudrna (1975) sunk *transiens* as junior subjective synonym of *Gonepteryx rhamni meridionalis* Röber, 1909.

**transiens** (sf)—*Leptidea sinapis transiens* Verity, 1916—033:98—Syntypes 10♂♂, 1♀ [England: Southampton]: New Forest: 12-18 VII 1874: Conquest [leg.].

**transiensrhamni** (ra)—*Gonepteryx rhamni transiensrhamni* Verity, 1947 [nec Verity & Linnaeus]—117:307—Syntype ♀ [Italy]: Marche: Bolognola: 30 VII 1937: Querci [leg.]—Name for transitional form ('race') published hyphenated.

**triangula** (ra)—*Euchloe belia occidentalis triangula* Verity, 1908—010:176—Syntype 1♂ Asia Minor: Akbes.

**triangulata** (if)—*Pieris rapae triangulata* Verity, 1917—034:180—[Italy]: Isola d'Elba(?).

**trimaculata** (fm)—*Pieris rapae trimaculata* Verity, 1908—010:155—Italy: Florence.

**tsinglingica** (ra)—*Pieris goutellei tsinglingica* Verity, 1911—010:326—[China]: Tsing-ling Mts.: Tai-pai-chan.

**uber** (if)—*Colias hyale calida uber* Verity, 1926—058:171—Syntype ♂ [Italy: Alpi Marittime: Terme di] Valdieri: 14 VIII [19]09: [Verity leg.]; type: *uber*.

**ubercalida** (if, sr)—*Colias hyale calida ubercalida* Verity, 1947—117:258—Syntypes 11♂♂, 3♀♀ [France]: A[lpes-]M[artimes]: Vence: [300 m]: 25 VIII-2 IX [19]37, 2 VII [19]31: Verity [leg.].

**ultimogenita** (nomen nudum)—*Pieris brassicae brassicae ultimogenita* Verity, 1947—117:247—Name for individual form published without description, definition or indication.

**umoris** (if, ra)—*Pieris napi vulgaris umoris* Verity, 1921—042:210—Syntypes 6♂♂, 6♀♀ [Italy: Toscana: Lucca]: Forte dei Marmi: 13-14 IV [1]900, 3-16 IV [19]12: [Verity leg.].

**urumtsiensis** (ra)—*Colias thisoa urumtsiensis* Verity, 1909—010:252—Thienshan Urumtsi.

**venata** (fm)—*Pieris brassicae brassicae venata* Verity, 1908—010:164—Morocco.

**veragra** (ra, sf)—*Pieris manni veragra* Verity, 1935—094:44—Syntypes 25♂♂, 15♀♀ [Switzerland]: Wallis: Martigny: 25 VII-19 VIII [19]32, 38 VI-10 VII [19]33: Verity [leg.].

**veragraalpigena** (sr)—*Pieris mannii alpigena veragraalpigena* Verity, 1947—117:230—Italy: Alpi Cozie: Meana di Susa: 700 m—Name for transitional subrace published hyphenated.

**verbani** (ra, sf)—*Pieris napi verbani* Verity, 1926—058:173—Syntypes 1♂, 3♀♀ [Italy: Alto Adige]: Lago Maggiore: [Mt.] Mottarone: 1450 m: 18-20 VII [19]22: [Verity leg.].

**verna** (sf)—*Colias myrmidone verna* Verity, 1911—010:358.

**vernalis** (fm)—*Colias hyale hyale vernalis* Verity, 1909—010:222—[U.S.S.R.]: Russia: Poltava.

**vernalis** (fm)—*Colias croceus vernalis* Verity, 1909—010:269—Italy: Florence.

**vernalis** (nomen nudum)—*Euchloe charlonia transcaspica vernalis* Verity, 1911—010:340—Name for seasonal form published without description, definition or indication.

**vernalisamplaautumnalis** (sf)—*Colias croceus vernalisamplaautumnalis* Verity, 1947—117:289—Italy: Firenze—Name published hyphenated.

**versa** (ra)—*Colias alpheraki alpherakyi versa* Verity, 1911—010:349—Pamir: Togus Bulak.

**vibilioides** (ra)—*Leptidea amurensis vibilioides* Verity, 1911—010:345—Syntypes 1♂, 1♀ [U.S.S.R.]: Amur: Novo-Riersk: 26 IV [19]08; Amur: Blagowoltschensk.

**viluiensoides** (ra)—*Colias hyperborea viluiensoides* Verity, 1909—010:250—[U.S.S.R.]: Irkutsk.

**virida** (if)—*Gonepteryx cleopatra europaeus virida* Verity, 1919—042:87—Syntype ♂ [Italy]: Firenze: Via Leone X: 6 III [19]13: [Verity leg.].

**viridissima** (nomen nudum)—*Gonepteryx rhamni viridissima* Verity, 1919—042:48—Name for individual form published without description, definition or indication.

**viridissima** (if)—*Gonepteryx rhamni transiens viridissima* Verity, 1947—117: 303—Syntypes 3♂♂, 1♀ [Italy: Toscana]: Firenze, Firenze: Pian di Mugnone: 25 III [19]03, 12 IV [19]18, 14 VI [19]37: [Verity leg.].

**vitimensis** (ra)—*Pieris napi frigida vitimensis* Verity, 1911—010:332—Syntype ♀ [U.S.S.R.: Transbaykal]: Witim.

**vivida** (fm)—*Pieris melete vivida* Verity, 1911—010:330.

**vivida** (fm)—*Pieris napi firgida vivida* Verity, 1911—010:334.

**vulgaris** (ra, sf)—*Pieris napi vulgaris* Verity, 1913—023:177—Syntype ♀ [Italy: Firenze]: Via Leone X: 5 IV [18]99: [Verity leg.]; type: *vulgaris*.

**VULGARIS** (ssp)—*Pieris napi vulgaris* Verity, 1916—033:77—Italy: Firenze: spring generation—Verity raised to subspecies-rank infrasubspecific name proposed earlier for seasonal form and race, with the same original combination; type-material apparently identical: Syntype ♀ [Italy: Firenze]: Via Leone X: 5 IV [18]99: [Verity leg.]; type: *vulgaris*.

**xanthochroa** (ra)—*Leptidea duponcheli xanthochroa* Verity, 1911—010:343—Syria: Cedres du Liban—Larsen (1974): *Leptidea duponcheli xanthochroa* [nec Verity], subspecies.

**yokohamae** (fm)—*Pieris rapae yokohamae* Verity, 1908—010:157—Syntypes 2♂♂ Japan: Yokohama.

**zellerica** (nomen nudum)—*Pontia daplidice zellerica* Verity, 1923—052:18—Replacement for name deemed junior homonym, published without description, definition or indication.

**zemblica** (ra)—*Colias nastes werdandi zemblica* Verity 1911—010:355—Novaja Zemlja.

## LIBYTHEIDAE

**albonervulata** (if)—*Libythea celtis albonervulata* Verity, 1950—118:5—Italy: Lazio: Monti Aurunzi: Valle del Petrella: 1200 m.

**latefulva** (if)—*Libythea celtis latefulva* Verity, 1950—118:6—N. Italy: Alto Adige: Bolzano.

**obscurenervulata** (if)—*Libythea celtis obscurenervulata* Verity, 1950—118:5—Italy: Sardegna: Lanusei.

**rubescens** (if)—*Libythea celtis rubescens* Verity, 1950—118:6.

**violacea** (if)—*Libythea celtis violacea* Verity, 1950—118:5—N. Italy: Alto Adige: Ponte all'Isarco.

## NYMPHALIDAE

**aethereaeformis** (if, sf)—*Melitaea phoebe aethereaeformis* Verity, 1919—042:183.

**ALAICOLA** (ssp)—*Argynnis aglaja alaicola* Verity, 1935—095:202—Syntypes 8♂♂ [U.S.S.R.: C. Asia]: Saraw[schan] sept.: Raigowodsk: VII.; Gouv. Syr Darja: Aulie Ata: Ala tau mont. occ.: 2500 m: VII.; [all] ex Bang-Haas.

**albatheia** (if)—*Apatura ilia albatheia* Verity, 1950—118:29—Syntype ♂ [Italy]: Lazio: Anticoli corr.: 18 VIII [19]39: Prola [leg.].

**albescens** (if)—*Argynnis aglaia albescens* Verity, 1904—004:55—Holotype ♀ [Italy: Pistoia]: Appennino Pistoiese: Abetone: 8 VIII [1]903: [Verity leg.].

**albescens** (if)—*Melitaea didyma albescens* Verity, 1917—034:184.

**albina** (if)—*Melitaea phoebe albina* Verity, 1904—004:54.

***alpiumlaranda** (ra)—*Argynnis niobe alpiumlaranda* Verity, 1929—074:243—Syntypes 5♂♂, 2♀♀ [N. Italy]: Lago Maggiore: Intra: Cannero: Passo di Colle: 1245 m: 6-7 VII 1922; Pian Quaggie: 950 m: 20-21 VI 1922; [all] Verity [leg.].

***alpiumlata** (ra)—*Argynnis niobe alpiumlata* Verity, 1929—074:242—Syntypes 6♂♂, 9♀♀ [N. Italy]: Alpi Pennine; Macugnagna: 1300 m: 13 VII [19]24, 1 VIII [19]28; Vanzone: 700 m: 5-25 VII [19]24, 20 VII-20 VIII [19]28; [all] Verity [leg.].

***alpiummixta** (ra)—*Argynnis adippe alpiummixta* Verity, 1936—094:84—Syntypes 12♂♂, 17♀♀ [Italy: Belluno]: Alpi Pennine: [Anzasca Valley]: Vanzone: 700 m: 12 VII-11 VIII [19]24, 20 VII-22 VIII [19]28: Verity [leg.].

***alpiumsisenna** (ra)—*Argynnis niobe alpiumsisenna* Verity, 1929—074:243—Syntypes 2♂♂, 1♀ [N. Italy]: Alpi Carniche: Sappada: 1300 m, S. Stefano di Cadore: 900 m: 16-21 VII [19]26: Verity [leg.].

**alpiumsisennaalpiumlaranda** (nomen nudum)—*Argynnis niobe alpiumsisenna-alpiumlaranda* Verity, 1936—094:82—Name for transitional mixed race published hyphenated without description, definition or indication.

***alpiumstricta** (ra)—*Argynnis niobe alpiumstricta* Verity, 1929—074:243—Syntypes 3♂♂, 1♀ [Italy: Tornio]: Alpi Cozie: Sestrieres: 2035 m: 8 VIII 1925: Verity [leg.].

***altapyrenaea** (ra)—*Argynnis niobe altapyrenaea* Verity, 1933—089:244—Syntypes 3♂♂ [France: Pyrenees]: Gedre: 2 VII [19]24, 16 VII & 17 VIII [19]29: Rondou leg.

**anteaceris** (sf)—*Neptis hylas anteaceris* Verity,1950—118:39—[U.S.S.R.]: Amur.

**antediniensis** (sf)—*Clossiana dia diniensis antediniensis* Verity, 1950—118:246—Syntypes 3♂♂, 1♀ [France]: A[lpes]-M[aritimes]: Vence: 25 IV [19]27, 10 & 17 IV [19]33, 11 V [19]31: Coll. Gazel.

**anticopupillata** (if)—*Fabriciana adippe anticopupillata* Verity, 1950—118:293.

**APPENNINICA** (ssp)—*Argynnis niobe appenninica* Verity, 1915—028:213—Syntypes 3♂♂, 2♀♀ [Italy: Toscana]: Appennino Pistoiese: Abetone: 1300 m: 4-7 VIII [1]903, 10 VII [19]12: [Verity leg.].

**APPENNINICOLA** (ssp)—*Argynnis aglaja appenninicola* Verity, 1915—028:213—Syntypes 2♂♂, 1♀ [Italy: Toscana]: Appennino Pistoiese: Abetone: [1200 m]: 10 VII [19]12: [Verity leg.].

***appenninigena** (ra)—*Melitaea didyma apenninigena* Verity, 1919—042:181—Syntypes 3♂♂, 8♀♀ Italia centrale: Lucca: Prato Fiorito: 1000 m: 27 VII-2 VIII [????], 6 VIII 1915: Querci [leg.].

***araratica** (ra)—*Melitaea didyma araratica* Verity, 1929—069:113—[Turkey]: Mt. Ararat: southern slopes.

***asiae** (ra)—*Melitaea athalia asiae* Verity, 1940—113:612—Syntypes 3♂♂, 1♀ [U.S.S.R.]: Primorskij Kraj: Minengebiet v. Sutschansky: 1925.

**asiaefrigida** (if)—*Melitaea athalia helvetica asiae asiaefrigida* Verity, 1940—113:613—Holotype ♂ Sib[iria] m[eridionalis].

***asiaepallens** (ra)—*Argynnis ino asiaepallens* Verity, 1933—087:93—Syntypes 4♂♂, 2♀♀ Chines. Turkestan: Tianchan mont. or.: Juldus Tal: 2500 m: VII: [ex Bang-Haas].

**atava** (if)—*Apatura iris atava* Verity, 1950—118:31.

**aterrimevittaa** (if)—*Melitaea athalia tenuis aterrimevittata* Verity, 1920—046:61.

**athalides** (hy)—*Melitaea athalides* Verity, 1919—042:194—Syntype ♂ [Italy]: Monti Sibillini: Bolognola: [1200 m]: 29 VI-25 VI 1918.

**atralpina** (nomen nudum)—*Melitaea didyma atralpina* Verity, 1929—069:89—Name of uncertain purpose published without description, definition or indication.

**atralpina** (sr, if)—*Melitaea didyma tarlonia atralpina* Verity, 1950—118:105—Syntype ♀ [N. Italy]: Alpi Pennine: Vanzone: 700 m: 28 VII [19]28: Verity [leg.].

**atrarubra** (if)—*Melitaea didyma atrarubra* Verity, 1929—069:75—Holotype ♂ [N. Italy]: Lago Maggiore: Trobaso: Renco: 260 m: 28 IV [19]27.

**atroviolacea** (if)—*Boloria pales atroviolacea* Verity, 1932—084:108—Syntype ♀ [Italy]: Alpi Cozie: Sestrieres: 2035 m: 8 VIII 1925: Verity [leg.].

**atroviridans** (if)—*Boloria pales atroviridans* Verity, 1932—084:108.

**atrovittata** (if)—*Melitaea athalia atrovittata* Turati & Verity, 1911—015:209—Syntype ♂ [Italy: Alpi Marittime]: Valdieri: 20 VII [19]11: [Verity leg.]; type: *atrovittata.*

***aureliaeformis** (ra)—*Melitaea athalia aureliaeformis* Verity, 1917—034:186—Syntypes 1♂, 1♀ [Italy]: Torino: Venaria Park.—Higgins (1955): *Mellicta britomartis aureliaeformis* [nec Verity], subspecies.

***aurelianigrobscura** (ra)—*Melitaea parthenie aurelianigrobscura* Verity, 1931—083:187—[Austria]: Wien.

***auriniabalcanica** (ra)—*Euphydryas aurinia auriniabalcanica* Verity, 1950—118:75—[Yugoslavia]: Istria: Mitterburg: 16 V.

**austera** (if)—*Melitaea parthenoides beata austera* Verity, 1940—113:681—Syntypes 1♂, 1♀ Spagna [= Spain]: Barcellona.

***australis** (ra)—*Melitaea cinxia australis* Verity, 1916—033:128—Syntype ♂ [Italy]: Firenze: 23 V [19]08: [Verity leg.]; type: *australis.*

***austreminens** (ra)—*Clossiana euphrosyne austreminens* Verity, 1950—118: 240—Syntypes 13♂♂, 1♀ [France]: Var: Roquebrune[-sur-Argent]: 15-21 IV [????], A[lpes]-M[aritimes]: 12 VI [19]30: Coll. J. Gazel; [Italy]; Torino: Casselette: Pendicu, Musine: 5 VI 1946, Colline di Gassino: 450 m: 25 IV 1946: Rocca [leg.].

***austriaca** (ra)—*Argynnis niobe austriaca* Verity, 1929—074:241—Syntypes 3♂♂,3♀♀ Austria infer[ior: Wien].

***austrobscura** (ra)—*Melitaea cinxia austrobscura* Verity, 1950—118:135—Syntypes 4♂♂, 3♀♀ [Italy]: Abruzzi: Gran Sasso: 1600 m: 1-6 VII 1939: Romei [leg.].

**austroneston** (sr)—*Clossiana euphrosyne neston austroneston* Verity, 1950—118:240—Syntypes 9♂♂ [N. Italy: Alpi Marittime]: Valdieri: VII [18]98, 27 VII-10 VIII [19]03, 14-27 VII [19]11: [Verity leg.].

***barcina** (ra)—*Apatura ilia barcina* Verity, 1927—064:176—Spain: Barcelona: S. Antoni de Villamajor—Manley & Allcard (1970): *Apatura ilia barcina* [nec Verity], subspecies.

**basiovalis** (if)—*Clossiana dia basiovalis* Verity, 1950—118:243.

**basiovalis** (if)—*Clossiana euphrosyne basiovalis* Verity, 1950—118:236.

***benacensis** (ra)—*Melitaea athalia benacensis* Verity, 1940—113:627—Syntypes 6♂♂, 3♀♀ [N. Italy]: M[onte] Baldo: 16-23 VII [19]29: Rocci [leg.].

**berisaliformis** (if)—*Melitaea athalia maxima berisaliformis* Verity, 1917—034: 186—Italy: Firenze: Fontebuona: 400 m.

**berisalella** (if)—*Melitaea dejone berisalii berisalella* Verity, 1935—094:76—Syntypes 11♂♂, 8♀♀ [Switzerland]: Valais: Martigny: 23 VI-18 VII [19]33: Verity [leg.]; some specimens with incomplete data.

**brevicauda** (sf)—*Charaxes jasius septentrionalis brevicauda* Verity, 1919—042:179.

**BRITANNA** (ssp)—*Melitaea athalia britanna* Verity, 1915—028:210—Syntypes 6♂♂, 3♀♀ [S.W. England: Plymouth]: Tavistock: 18 VI [19]07: Rogers [leg.]—Not considered worthy of recognition as subspecies by Higgins (1955).

**caldaria** (sf)—*Melitaea didyma protea caldaria* Verity, 1920—046:59—Syntypes 2♂♂, 2♀♀ [France]: Nizza: [Montferrato]: 12 VIII 1904; [Italy: Alessandria]: Nuove Bagni di Aqui: 8 VIII 1912; some specimens with incomplete data.

**caldariepar** (ra, sf)—*Melitaea didyma caldariepar* Verity, 1950—118:121—Syntypes 2♂♂, 2♀♀ [France]: Nizza: [Montferrato]: 12 VIII 1904; [Italy: Alessandria]: Nuove Bagni di Acqui: 8 VIII 1912; some specimens with incomplete data.

**carbonaria** (if, sf)—*Polygonia c-album carbonaria* Verity, 1916—033:100—Syntype ♀ [Italy: Alpi Marittime]: Valdieri: [Verity leg.].

**CARPETANA** (nn)—*Melitaea cinxia carpetana* Verity, 1929—069:132—Replacement name for *Melitaea cinxia castiliana* Turati, 1920, which Verity considered junior primary homonym of *Melitaea didyma castiliana* Melcon, 1910; Higgins (1941) sunk *carpetana* as junior subjective synonym of an infrasubspecific 'modification' of *Melitaea cinxia* (Linnaeus, 1758).

***carsicola** (ra)—*Melitaea parthenia carsicola* Verity, 1932—083:29—Syntypes 8♂♂ [Italy]: Costa Trieste: Venezia Guilia: Carso: Opicina: 23-31 V [1]926.

**castanea** (if)—*Polygonia c-album castanea* Verity, 1950—118:346—Holotype ♂ [Italy]: Sardegna: Cagliari; 'olotipo': *castanea*.

**catamesoides** (sf, ra)—*Melitaea trivia trivia catamesoides* Verity, 1950—118:97—Syntypes 4♂♂, 1♀ [Italy]: Trieste: 2 VI [????]; [Trieste]: Carso: Redipuglia: 5 VIII [19]24: Rocci [leg.].

**cataminuta** (sf)—*Melitaea didyma cataprotea cataminuta* Verity, 1929—069: 118—Syntypes 3♂♂, 1♀ [Spain: Catalonia: Barcelona]: Vallvidiera: IX 1921, La Garriga: IX 1921, 2-14 IX 1922.

**catananoides** (sr, sf)—*Melitaea trivia trivia catananoides* Verity, 1950—118:97—[Italy]: Roma: Paliano, Fonte Nuova di Fiuggi; Abruzzi: Gran Sasso: Casteldelmonte: 1400 m.

**cataoccasus** (sf, if)—*Melitaea didyma cataprotea cataoccasus* Verity, 1929—069:118—Syntypes 9♂♂, 5♀♀ [Spain: Catalonia: Barcelona]: La Garriga: 10-20 VII 1922.

***cataprotea** (ra)—*Melitaea didyma cataprotea* Verity, 1929—69:117—Syntypes 2♂♂, 1♀ [Spain: Catalonia: Barcelona]: Vallvidrera: V-10 VI 1922.

***caucasi** (ra)—*Melitaea trivia caucasi* Verity, 1922—042:13—Syntypes 1♂, 1♀ [U.S.S.R.]: Caucasso: Latpari Pass: 2000 m: 4 VIII 1890.

**CAUCASICOLA** (nn)—*Melitaea phoebe caucasicola* Verity, 1919—042:184—Replacement name for *Melitaea phoebe caucasica* Staudinger, 1870, said to be junior primary homnym of *Melitaea didyma caucasica* Staudinger, 1861; since the junior homonym was laready replaced with *Melitaea phoebe ottonis* Fruhstorfer, 1916, Verity's name is junior objective synonym of the original replacement name of Fruhstorfer; Higgins (1941) treated this taxon as 'modification' (infrasubspecific form).

**CAUCASOGENITA** (nn)—*Melitaea athalia caucasogenita* Verity, 1930—078: 134—Replacement name for *Melitaea athalia caucasica* Staudinger, 1871, said to be primary junior homonym of *Melitaea didyma caucasica* Staudinger, 1861; taxonomic status of *caucasogenita* is uncertain; it was not treated as subspecies by Higgins (1941).

***cebenica** (ra)—*Argynnis niobe cebenica* Verity, 1929—074:243—Syntypes 2♀♀ [France]: Lozere: Cevenes: Concoules: Bergerie: Malmontet: 14 VII [19]24.

**celladdita** (if)—*Melitaea didyma celladdita* Verity, 1950—118:106—Syntype ♀ [Italy: Lucca]: Pratofiorito: 6 VIII [1915].

**cellapartita** (if)—*Melitaea didyma cellapartita* Verity, 1950—118:106—Syntype ♂ Italia centrale: Firenze: Pian d Mugnone: 200 m: 29 V 1915: Querci [leg.].

***centralitaliae** (ra)—*Limenitis camila centralitaliae* Verity, 1950—118:49—Syntypes 12♂♂, 1♀ Italia centrale: Toscana: Livorno: Tombolo: 9 VIII 1917: Verity [leg.]; [Italy]: Suditalia: [Lazio]: Valle Moltarino: Massicchio delle Mainarde: 500 m: 3 VII 191[?]: Querci [leg.].

**chitralipluvia** (sf)—*Melitaea didyma chitralensis chitralipluvia* Verity, 1929—069:43—Syntypes 1♂, 1♀ [Pakistan]: Chitral: Utzen nallah: 7-10000 ft.: 8 VII [19]03: Saunders [leg.]; Chitral: Shishi Kuh Valley: 9-14000 ft.: Colomb [leg.]; both specimens ex BM(NH): 1904-237, 99-65.

**clara** (if)—*Apatura ilia clara* Verity, 1950—118:24.

***clarens** (ra)—*Argynnis esperi clarens* Verity, 1919—042:196—Syntype ♂ Italia centrale: Toscana: Colline di Firenze: 400 m: 12 VII 1914: Querci [leg.]; type: *clarens*.

***comacinaaurinia** (ra)—*Eyphydryas aurinia comacinaaurinia* Verity, 1950—118:76—[Switzerland]: Bellinzona: Motto d'Arbino: 1700 m: 25 VI [????]—Verity published this name hyphenated and attributed the authorship erroneously to 'Trti-Rott.'.

**communis** (sf, ra)—*Melitaea parthenoides completa communis* Verity, 1931—083:137—Syntypes 3♂♂, 1♀ France: [Maine-et-Loire]: Angers.

***completa** (ra)—*Melitaea parthenoides completa* Verity, 1931—083:136—Syntype 1♂ [France: Paris]: Fountainebleau: [illegible]: VIII [19]19.

***composita** (ra)—*Melitaea diamina composita* Verity, 1935—094:72—Syntypes 8♂♂, 1♀ [Switzerland]: Vaud: [Martigny]: Pont de Nant: 4-25 VII [19]33, 11 VII [19]33: Verity [leg.].

**conjuncta** (if)—*Pyrameis cardui conjuncta* Verity, 1919—042:197—Holotype(?) ♂ Type: *conjuncta*; other data not stated.

**contracta** (if)—*Melitaea didyma contracta* Verity, 1950—118:108.

***coreae** (ra)—*Melitaea britomartis coreae* Verity, 1930—078:82—Syntypes 1♂, 2♀♀ Coree [= Korea]: Coll. Deckert—Original combination very confused: called 'race' and by implication belongs to *britomartis*.

**COREAE** (sp)—*Melitaea coreae* Verity, 1940—113:646—Syntypes 1♂, 1♀ Coree [= Korea]: Coll. Deckert—Verity raised to species-rank his race *coreae*; sunk as junior subjective synonym of *Mellicta britomartis latefasciata* (Fixen, 1883) by Higgins (1955).

**corythalia** (if)—*Melitaea britomartis corythalia* Verity 1950—118:187—Holotype ♂ [Italy: Milano]: Turbigo: 9 VII [19]30: Rocci [leg.]; 'olotipo': *corythalia*.

**crassenigra** (ra, if)—*Melitaea phoebe crassenigra* Verity, 1928—058:162—Syntypes 3♂♂, 2♀♀ [France]: Loz[ere] & Avey[ron]: Le Rozier: to 1800 ft.: 10-15 VII 1926: Graves [leg.]; [Pyrenees]: Ambollos: VI! [19]14; Bordeaux: Pessac: 23 VIII [19]14; Gironde: Villenave.

**crassepicta** (if)—*Melitaea ambigua kenteana crassepicta* Verity, 1940—113: 600—Holotype ♂ Altai; tipo: *crassepicta*; ex coll. Grum-Grshimailo, via coll. Elwes, via BM(NH); 1902-85 in coll. Verity.

**crassepicta** (if)—*Melitaea parthenoides completa crassepicta* Verity, 1950—118:202.

***creta** (ra)—*Vanessa antiopa creta* Verity, 1916—033:101—Syntypes 3♂♂, 1♀ [Italy: Toscana]: Firenze: Cascine, Monte Senario: 5 III 1903, 11 VII [19]04, ex larva 1903: [Verity leg.].

**cymothoe** (if)—*Melitaea varia cymothoe* Verity, 1950 [nec 1931]—118:203—Syntype ♀ [France]: Gallia mer.: St. Martin-Ves[ubie]: 2100 m: 24 VIII [????]: Coll. Höfer, Wien.

**cymothoe** (if)—*Melitaea britomartis cymothoe* Verity, 1950—118:187—Syntype ♂ [Italy: Milano]: Turbigo: 29 V [19]30: Rocci [leg.].

***debilisprovincialis** (ra)—*Melitaea aurinia debilisprovincialis* Verity, 1928—068:90—Syntypes 18♂♂, 1♀ France: Gironde: St. Come Bazas: 26 IV 1923-8 V [19]24 [various dates]: Sorin [leg.]; some specimens with incomplete data.

**DEJONEFORMIS** (nn)—*Melitaea athalia dejoneformis* Verity, 1915—028:208—Replacement name for *Melitaea deione nevadensis* Oberthür, 1904, said to be preoccuied by *Melitaea parthenie nevadensis* Spuler, [1901, nec 1908], as pointed out also by Higgins (1955); Verity (113:615) spelled the name *deioneformis*; it appears that Spuler's name was published in 1901.

**dejonella** (sf)—*Melitaea dejone dejonella* Verity, 1930—078:134—France: Var: St. Zacharie.

**deleta** (if)—*Melitaea phoebe tusca deleta* Verity, 1919—042:184.

**deletasicca** (if)—*Melitaea didyma deletasicca* Verity, 1950—118:107.

***demissa** (ra)—*Eyphydryas cynthia demissa* Verity, 1950—118:83—Syntypes 3♂♂, 2♀♀ [N. I]: Trentino: Lago Serodoli: Madona di Campiglio: 2200 m; [Alpi Retiche]: Spluga: VIII [19]20: Costantini [leg.]; [Alpi Retiche]: Bormio: 2000 m: 21 VII[19]33: Rocci [leg.].

**DIAMINOIDES** (nn)—*Melitaea athalia diaminoides* Verity, 1940—113:635—Replacement name for *Melitaea athalia dictynnoides* Fruhstorfer, 1917, which Verity erroneously considered invalid primary junior homonym of *Melitaea aurelia dictynnoides* Hormuzaki, 1898; Verity's action was unnecessary since Fruhstorfer referred *dictynnoides* to Hormuzaki, as already correctly pointed out by Higgins (1955).

**dorfmeisteri** (if)—*Melitaea parthenie dorfmeisteri* Verity, 1950—118:191—Germany: Südbayern.

**emicandida** (if)—*Melitaea didyma emicandida* Verity, 1911—016:266—Holotype ♂ [Italy: Toscana: Firenze]: Vallombrosa: VIII 1905; type: *emicandida*.

**emielymi** (if)—*Pyrameis cardui emielymi* Verity, 1919—042:198—Holotype ♀ [Italy: Toscana: Firenze]: Vallmbrosa: VIII 1905: Verity [leg.]; type: *emielymi*.

***emiflorens** (ra)—*Issoria lathonia emiflorens* Verity, 1919—042:195—Syntypes 1♂, 1♀ Italia centrale: Lucca: Fiume Camaione: 300 m: 27 VIII 1915: Querci [leg.]—Name proposed for 'transitional race' (form).

***emilocuples** (ra)—*Argynnis aglaja emilocuples* Verity, 1919—042:195—Syntypes 1♂, 1♀ [Germany]: Berlin.

**emilocupleslocupletata** (nomen nudum)—*Argynnis aglaja emilocupleslocupletata* Verity, 1935—095:203—Name for transitional or mixed race published without description, definition or indication.

**emilocupleslocupletata** (sr)—*Mesoacidalia charlotta locupletata emilocupleslocupletata* Verity, 1950—118:303—Syntypes 13♂♂, 3♀♀ [N. Italy]: Sulden: Ortler: 1800 m: 3-10 VIII [19]20, 4-6 VIII 1933: Verity, Taccani [leg.]; Alto Adige: Trafoi: [1500 m]; some specimens with incomplete data.

***eminens** (ra)—*Boloria euphrosyne eminens* Verity, 1932—086:113—Syntypes 5♂♂ [France]: H[autes]-P[yernees]: Gedre: VI [19]16: Rondou [leg.]; some specimens with incomplete data.

**emipauper** (sf)—*Melitaea phoebe tusca emipauper* Verity, 1919—042:183—Syntypes 2♂♂ [Italy]: Toscana: Firenze: Vallombrosa: VIII 1905: Verity [leg.].

***emipunica** (ra)—*Melitaea phoebe emipunica* Verity, 1919—042:184—Syntypes 4♂♂, 1♀ [Italy]: Isola di Sicilia: Palermo: Monreale: San Marino: 800 m: 3-5 V 1918, 1-2 V [19]17: Querci [leg.]; some specimens with incomplete or abbreviated data.

**ESPERI** (nn)—*Argynnis esperi* Verity, 1913—022:205, 023:183—Replacement name or *Papilio cydippe* Linnaeus, 1761; Verity considered *Papilio adippe* Denis & Schiffermuller, 1775, unavailable for the same species.

**europaeus** (nomen nudum)—*Charaxes jassius europaeus* Verity, 1917—034:182—Name for race published without description, definition or indication.

**evittata** (if)—*Melitaea athalia maxima evittata* Verity, 1917—034:187—Italy: Isola d'Elba.

**flavens** (sf)—*Brenthis dia laetior flavens* Verity, 1919—042:194—Syntypes 2♂♂ Italia centrale: Toscana: [Firenze]: Fiesole: Monte Senario: 700 m: 12 VII 1918: Verity [leg.].

**flavescens** (if)—*Charaxes jasius flavescens* Verity, 1950—118:18.

**FLORENS** (ssp)—*Argynnis lathonia florens* Verity, 1916—033:130—Syntypes 1♂, 1♀ [Italy: Toscana]: Firenze: Vallombrosa: [1000 m]: VIII 1905: M[onte] Fanna: 600 m: 1 IX [19]13: Verity [leg.].

***florida** (ra)—*Brenthis hecate florida* Verity, 1919—042:195—Syntypes 7♂♂, 4♀♀ Italia centrale: Firenze: Pian di Mugnone: 200 m: 25 VI [18]99, 25 VI [19]01, V [19]04, 13 VI 1915, 25 VI 1917, 15-24 VI 1919: Querci, Verity [leg.]; some specimens with incomplete or poorly legible data.

**folvonigrolimbata** (if)—*Melitaea didyma folvonigrolimbata* Verity, 1950—118: 110—[Italy: Toscana]: Forte dei Marmi: 8 VII [????]; figured as *fulvonigrolimbato* pl. 41 fig. 46.

**forcipigerans** (if)—*Charaxes jasius forcipigerans* Verity, 1950—118:18.

***frigidaltaica** (ra)—*Melitaea britomartis frigidaltaica* Verity, 1940—113:656—Syntypes(?) 11♂♂ [U.S.S.R.]: Altai centr. mont.: [ex Bang-Haas]; Verity mentioned 'type' in the original description, but the type-series contains no specimen labelled 'type' or holotype.

***frigidescens** (ra)—*Melitaea aurinia frigidescens* Verity, 1928—068:45—Syntype ♂ [Switzerland]: Vallese: [Martigny]: Wulfschlegel [leg.].

**fulvobscura** (if)—*Apatura ilia fulvobscura* Verity, 1950—118:24.

**fulvoclara** (if)—*Apatura ilia fulvoclara* Verity, 1950—118:24.

**fulvunicolor** (if)—*Euphydryas ichnea fulvunicolor* Verity, 1950—118:85—Syntypes 9♂♂ [China]: Manciukuo: Yablonya [leg.].

**fulvuniformis** (if)—*Euphydryas ichnea fulvuniformis* Verity, 1950—118:86—Syntypes 2♂♂ [Italy]: Alpi Dolom[ite]: Val Gres[so]: Pian delle Giare: 1300 m: 26 VI 1938: Rocca [leg.]; [N. Italy]: Sappada: 20 VII 1936: Rocci [leg.].

***fuscans** (ra)—*Argynnis aglaja fuscans* Verity, 1935—095:190—Syntypes 12♂♂, 1♀ [N. Italy]: Alpi Carniche: Sappada: 1300 m: 21 VII-6 VIII [19]26; S. Stefano di Cadore: 900 m: 17 VII [19]26: [all] Verity [leg.].

**fuscata** (sr)—*Boloria pales palustris fuscata* Verity, 1950—118:222—Syntypes 8♂♂, 7♀♀ [Italy: Sutirol]: Sulden: Ortler: 1800 m: 3-10 VIII [19]20: Verity [leg.].

**fuscissima** (if)—*Melitaea parthenie fuscissima* Verity, 1950—118:190—Holotype ♂ [N. Italy: Torino]: Alpi Cozie: Val Susa: 1100 m: Oulx [= Ulzio]: 6 VII 1925: Verity [leg.]; this holotype is also syntype of *Melitaea parthenie imitatrix* Verity, 1935.

***galliaemontium** (ra)—*Melitaea phoebe galliaemontium* Verity, 1928—058: 162—France: Auvergne: Mt. Dore.

***garumma** (ra)—*Melitaea didyma garumma* Verity, 1929—069:72—France: Pyrenees-Orientales: Vernet-les-Bains.

**georginigrior** (sf)—*Melitaea didyma georgi georginigrior* Verity, 1950—118: 124—N. Italy: Lago Maggiore: Intra: Piazza di Armi.

**GIGASVITATHA** (ssp)—*Argynnis aglaja gigasvitatha* Verity, 1935—095:202—Syntypes 3♂♂, 4♀♀ [U.S.S.R.: C. Asia]: Issyk kul mer.: sudl. Narynsk: Karagaitau Gbg.: Juli: [ex Bang-Haas].

**GLACIEGENITA** (nn)—*Melitaea aurinia glaciegenita* Verity, 1928—068:43—Replacement name for *Papilio merope* Prunner 1798 preoccupied by *Papilio merope* Fabricius, 1775; Verity gave *glaciegenita* the rank of 'exerge'—to be interpreted as subspecies—and drew attention to its possible specific rank; designation of 'cotypes' made by Verity is invalid: 1♂, 1♀ Italia settentrionale: Alto Adige: Stelvio [Pass]: VII 1920: Astaller [leg.]—Since *Melitaea artemis merope debilis* Oberthür, 1909, was published without description, definition or indication (nomen nudum) and was specifically proposed for an aberration (unavailable infrasubspecific name), the name *glaciegenita* appears to be the oldest available name for the taxon: an alpine species (or subspecies?) closely related to *Euphydryas aurinia* (Rottemburg 1775), described by Higgins (1950), figured by Forster & Wohlfahrt (1976) and Higgins & Riley (1980)—Correct combination at present: *Euphydryas glaciegenita* (Verity 1928) if treated as species or *Euphydryas aurinia glaciegenita* (Verity 1928) if considered of subspecies-rank; species-rank is probably correct treatment of this taxonomically difficult taxon.

**graecaeformis** (if)—*Melitaea didyma protea graecaeformis* Verity, 1917—034: 183—Italy: Toscana: Poggio.

**griseopicta** (if)—*Melitaea phoebe griseopicta* Verity, 1950—118:149.

**hiberava** (if)—*Melitaea didyma hiberava* Verity, 1929—069:130—Holotype ♀ [Spain: Aragon]: [Teruel]: Orihuela: 1700 m: 14 VII [19]24: Querci [leg.].

**hypererythra** (if)—*Limenitis anonyma hypererythra* Verity, 1950—118:52.

**HYPOARSILACHE** (nn)—*Boloria pales hypoarsilache* Verity 1932—084:106—Replacement name for *Argynnis pales lapponica* Staudinger, 1861 said to be secondary junior homonym of *Boloria dia lapponica* (Esper, 1790). Later sunk by Warren (1944).

**hypoerythra** (if)—*Limenitis anonyma hypoerythra* Verity, 1950—118:52.

**IBERAGIGAS** (nn)—*Melitaea athalia iberagigas* Verity, 1930—078:134—Replacement name for *Melitaea athalia iberica* Staudinger, 1901 which is preoccupied by *Melitaea aurinia iberica* Oberthür, 1881; the junior primary homonym was replaced earlier by *Melitaea athalia hispanica* Wnukowsky, 1929.

**iberanana** (sf, ra)—*Melitaea athalia iberagigas iberanana* Verity, 1930—078: 135—Syntypes(?) 8♂♂, 9♀♀ Portugal: Serra da Estrela: 800-1000 m: 24 VII-20 VIII 1927: Querci [leg.]—Belongs to *M. deione* (Geyer, 1832).

**infrabrunnea** (nomen nudum)—*Pyrameis cardui infrabrunnea* Verity, 1919—042:198—Name for individual form published without description, definition or indication.

**infraconfluens** (if)—*Charaxes jasius infraconfluens* Verity, 1950—118:18.

**infracrasselunata** (if)—*Melitaea didyma infracrasselunata* Verity, 1950—118: 110—Holotype ♂ [N. Italy]: Alpi Retiche: Bormio: 1300 m: 5 VII 1927: Verity [leg.].

**infraflava** (nomen nudum)—*Pyrameis cardui infraflava* Verity, 1919—042:198—Name for individual form published without description, definition or indication.

**infraflava** (if)—*Euphydryas aurinia infraflava* Verity, 1950—118:71.

**infragrisea** (nomen nudum)—*Pyrameis cardui infragrisea* Verity, 1919—042: 198—Name for individual form published without description, definition or indication.

**infrajuncta** (if)—*Melitaea trivia infrajuncta* Verity, 1950—118:98—Holotype ♂ [N. Italy]: Alpi Cozie: Val Susa: Meana M.: 700 m: 27 VII 1940: Rocca [leg.].

**inframedioconfluens** (if)—*Melitaea didyma inframedioconfluens* Verity, 1950—118:110.

**infranigrans** (nomen nudum)—*Pyrameis cardui infranigrans* Verity, 1919—042:198—Name for individual form published without description, definition or indication.

**infranigrans** (if)—*Limenitis populi bucoviensis infranigrans* Verity, 1950—118:58—Syntype ♂ [Italy]: Trentino: Val Genova: 10 VII [1]946: Fiori [leg.].

**infraochracea** (nomen nudum)—*Pyrameis cardui infraochracea* Verity, 1919—

042:198—Name for individual form published without description, definition or indication.

**infraochrea** (if)—*Euphydryas aurinia infraochrea* Verity, 1950—118:71.

**infrapallida** (if)—*Boloria napaea napaea infrapallida* Verity, 1950—118:214—Syntypes 1♂, 1♀ [N. Italy]: Alpi Cozie: Sestrieres: 2035 m: 8 VIII 1925: Verity [leg.].

**ignea** (sf)—*Melitaea didyma ignea* Verity, 1929—069:74—N. Italy: Lago Maggiore: Intra.

***imitans** (ra)—*Melitaea britomartis imitans* Verity, 1930—078:83—U.S.S.R.: Tchita.

***imitatrix** (ra)—*Melitaea parthenie imitatrix* Verity, 1932—083:28—Syntypes 19♂♂,12♀♀ [N. Italy]: Alpi Cozie: Val Susa: Oulx [= Ulzio]: 1100 m: 30 VI-19 VII [19]25: Verity [leg.].

***inanis** (ra)—*Melitaea parthenie inanis* Verity, 1921—042:213—Syntypes 12♂♂, 6♀♀ [France]: Eure: Pont-de-l'Arche.

**inops** (if)—*Pyrameis cardui inops* Verity, 1919—042:198—Holotype ♂ [Italy: Toscana]: Forte dei Marmi: 25 VIII [1]900: [Verity leg.].

***isarcica** (ra)—*Melitaea diamina isarcia* Verity, 1931—082:68—Syntypes 3♂♂ [Italy]: Südtirol: Bozen: Chiusa [= Klausen]: 520 m: VII 1918.

***laetior** (ra)—*Brenthis dia laetior* Verity, 1919—042:194—Syntypes 1♂, 1♀ Italia centrale: Toscana: Firenze: Pian [di] Mugnone: 200 m: 23 IV 1918: Querci [leg.].

**larandaherse** (sr)—*Fabriciana niobe larandaherse* Verity, 1952—116:395—Name for subrace(?) published without description, definition or indication.

**latealba** (if)—*Limenitis camilla latealba* Verity, 1950—118:46—Holotype ♂ [France]: Eure: Pont-de-l'Arche: VII 1933; 'olotipo' *latealba*.

**laterubra** (if)—*Boloria napaea napaea laterubra* Verity, 1950—118:214—Holotype ♂ [N. Italy]: Alpi Cozie: Sestrieres: 2035 m: 8 VIII 1925: Verity [leg.].

**latevirida** (if)—*Boloria napaea latevirida* Verity, 1950—118:214.

**leopardata** (if)—*Melitaea didyma caldaria leopardata* Verity, 1924—052:37—Syntypes 2♀♀ [Italy]: Elba: VIII [1]908.

***lesoralpina** (ra)—*Melitaea didyma lesoralpina* Verity, 1950—118:128—Syntypes 10♂♂, 4♀♀ [Italy]: Alpi Carniche: Val Piave: Sappada: 1200-1800 m: 8-29 VII [19]36, 23 VI [19]34, 8 VIII [19]33: Rocci, Rocca [leg.].

**l-extincta** (if)—*Polygonia egea l-extincta* Verity, 1950—118:343—Holotype ♂ [Italy]: Firenze: Stefan[elli leg.]; 'olotipo': *l-extincta*.

**limboextans** (if)—*Charaxes jasius limboextans* Verity, 1950—118:18—Holotype(?) ♂ [Italy]: Costa Toscana: Viareggio: Facette: 4 V [19]28: ex larva: Verity.

***limeraparthenoidemima** (ra)—*Melitaea athalia limeraparthenoidemima* Verity, 1939—109:19—Syntypes 4♂♂, 2♀♀ Bulgaria occ.: Rilo D[agh]: Krilova Pol.: 1500 m: 18 VI-2 VIII [19]28: Coll. Züllich.

***locuples** (ra)—*Argynnis aglaja locuples* Verity, 1919—042:195—Syntypes 4♂♂, 2♀♀ [N. Italy: Alpi Marittime]: Valdieri: VIII [18]98, 15-20 VIII 1909: [Verity leg.].

***locupletata** (nn)—*Argynnis aglaia locupletata* Verity, 1922—042:15—Replacement name for (unavailable infrasubspecific name) *Argynnis aglaja locuples* Verity, 1919 said to be primary junior homonym of (available name) *Argynnis adippe locuples* Butler, 1881.

***lucasi** (ra)—*Melitaea aurelia lucasi* Verity, 1920—045:274—Syntypes 4♂♂, 3♀♀ [France]: Oise: Morevil: Plateau St. Claude: 22-29 VI 1919, 1 VII 1919.

**lucida** (if)—*Melitaea didyma lucida* Verity, 1950—118:108—Holotype(?) ♂ It[alia] cent[rale]: Antico Gretto dell'Arno: Marina di Pisa: 25 V 1917: Verity [leg.]; 'olotipo': *lucida.*

**luteissima** (if)—*Apatura ilia luteissima* Verity, 191—042:178—Holotype ♂ [Germany]: Prussia: Düsseldorf; type: *luteissima.*

***magisnigrata** (ra)—*Argynnis lathonia magisnigrata* Verity, 1933—088:58—Syntypes 10♂♂, 5♀♀ [N. Italy]: Alpi Pennine: Vanzone: 700 m: 16 VII-18 VIII [19]24: 7 VII-3 VIII [19]28: Verity [leg.].

***magnacasta** (ra)—*Melitaea didyma magnacasta* Verity, 1929—069:128—Holotype ♀ Persia; 'olotipo': *magnacasta*; described from a single specimen.

***magnaclara** (ra)—*Melitaea diamina magnaclara* Verity, 1931—082:68—Syntypes 15♂♂, 4♀♀ [Italy: Alpi-Marittime]: Valdieri: [18]98-[19]11 [various dates, illegible: Verity leg.].

***magnaclara** (ra)—*Boloria euphrosyne magnaclara* Verity, 1932—086:120—Turkey: Amasia.

***magnaclarens** (ra)—*Argynnis adippe magnaclarens* Verity, 1936—094:85—Holotype ♂ [France]: Gard: Pont-St.-Esprit: La Valbourne: 11 VII [19]26: Gaillard [leg.]; original rank uncertain, presumably race.

**magnaestiva** (sf)—*Melitaea didyma subpatycosana magnaestive* Verity, 1929—069:76—Syntypes 5♂♂, 7♀♀ [France]: Montepellier: Marais a Montes: 24 VI [19]28: Gaillard [leg.]; [Montepellier/Nimes]: Gallargues: [Vidourle River]: 31 VIII [19]24; Bouches-du-Rhone: 7 VIII [19]20.

***magnaobscura** (ra)—*Melitaea diamina magnaobscura* Verity, 1931—082:80—Syntypes 7♂♂, 2♀♀ [France]: Gironde: Bordeaux: 10-17 VI [19]24, 19 VI 1923, 1922, 17 VI 1929; Gironde: Marais: Villenave: 4 VI [19]25, 4 VI [19]29.

***magnata** (ra)—*Dryas paphia magnata* Verity, 1919—042:196—Syntypes 3♂♂ France: Maine-et-Loire: Les Bourtardieres: 1-8 VII 1917: Querci [leg.].

***magnifica** (ra)—*Dryas paphia magnifica* Verity, 1919—042:196—Syntpes 3♂♂ [Italy: Toscana]: Firenze: [Giogoli]: Collazzi: 300 m; Cascine: VII [1]903; Via Leone X: 7 VII [18]99; [Verity leg.].

***magnificamagnata** (ra)—*Argynnis paphia magnificamagnata* Verity, 1950—118:311—Syntypes 3♂♂ [France]: A[lpes]-M[aritimes]: Vence: 20 VIII [19]37; St. Barnabe: 17 VIII [19]37: Verity [leg.].

**majacyrnea** (sr)—*Pandoriana maja maja majacyrnea* Verity, 1950—118:318—Syntypes 4♂♂ [Italy: Isola d']Elba: VII [19]09.

***majuscula** (ra)—*Argynnis hecate majuscula* Verity, 1933—092:174—Syntypes 2♂♂ [Romania]: Hermannstadt [= Sibiu]: 17 VI [19]12, 19 VI [19]21.

**maxima** (if)—*Boloria pales maxima* Verity, 1950—118:217.

***maximemaculosa** (ra)—*Argynnis lathonia maximemaculosa* Verity, 1933—088:58—Syntype ♂ [Switzerland]: Vaud: Bex: 28 VII-3 VIII [19]32: Verity [leg.].

**medioduplicata** (if)—*Melitaea didyma medioduplicata* Verity, 1950—118:106—Holotype ♀ [Italy]: Is[ola] d'Elba; 'olotipo': *medioduplicata.*

**medioastricta** (if)—*Melitaea phoebe medioastricta* Verity, 1950—118:148—Syntype ♂ [N. Italy]: Lago Maggiore: Intra: 200 m: 28 IV-4 V [19]27.

***microdelminia** (ra)—*Melitaea athalia microdelninia* Verity, 1940—113:628—Holotype ♂ Italia settentrionale: [Bozen]: Mendola Pass: 21 VII [19]20.

**microignasiti** (sf, if)—*Melitaea trivia ignasiti microignasiti* Verity, 1950—118:97—Syntypes 15♂♂, 8♀♀ Portugal: Serra da Estrela: 800-100 m: 18 VII-12 VIII 1927, 21 IX 1927: Querci [leg.].

**microleopardata** (sf, if)—*Melitaea didyma microleopardata* Verity, 1929—069:76—Syntypes 10♀♀ [France]: Lot: Douelles; all specimens under one group-label.

***micromelanica** (ra)—*Melitaea parthenie micromelanica* Verity, 1935—094:73—Syntypes 3♂♂ [Switzerland]: Valais: Sierre [= Pfynwald]: 29 VIII 1932: Verity [leg.].

**microrovia** (if)—*Melitaea phoebe rovia microrovia* Verity, 1950—118:157—Syntypes 92♂♂, 3♀♀ N. Italy: [various localities]; [Yugoslavia]: Istria: Portorosa.

***microsyriaca** (ra)—*Melitaea trivia microsyriaca* Verity, 1950—118:96—Syntypes 3♂♂, 2♀♀ Persia: Monti Schahkuh; Palestina: Aiklit: 29 VI [19]28, Aleih: 28 VII [19]31: Ellison [leg.]; Siria.

**microtitania** (if, ra)—*Boloria aathusia titania microtitania* Verity, 1933—087:91—Syntypes 2♂♂ [N. Italy]: Alpi Cozie: Cesana Torin.: 1300 m: 24 VII 1925: Verity [leg.].

**minor** (if)—*Euphydryas cynthia minor* Verity, 1950—118:81.

**minutior** (nomen nudum)—*Pyrameis atalanta minutior* Verity, 1924—052:42—Name for race or ecological form published without description, definition or indication.

**minutior** (sr)—*Vanessa atalanta italica minutior* Verity, 1950—118:340—Italy: Livorno: Quercinella.

***mixtaceladussa** (ra)—*Melitaea athalia mixtaceladussa* Verity, 1940—113:625—Syntypes 4♂♂, 1♀ [France]: H[autes]-P[yrenees]: Gedre: VI [19]15, 15 VI [19]16, VII [19]16: Rondou [leg.].

***mixtalpicola** (ra)—*Melitaea athalia mixtalpicola* Verity, 1940—113:626—Switzerland: Grisons: Pontresina: 2000 m.

**modesta** (sr)—*Boloria napaea napaea modesta* Verity, 1950—118:216—Syntypes 22♂♂, 28♀♀ [N. Italy]: Alpi Cozie: Sestrieres: 2035 m: 8 VIII 1925; Clavieres: 1800 m: 29 VII 1925; Sulden: Ortler: 1800 m: 3-10 VIII [19]20; Alpi Retiche: Stelvio: 2300 m: 10 VIII [19]27; [all] Verity [leg.].

***monilata** (ra)—*Melitaea phoebe monilata* Verity, 1919—042:184—Syntypes 2♂♂, 1♀ [Switzerland]: Vallese: Wulfschlegel [leg.].

**monilataeformis** (if)—*Melitaea phoebe tusca manilataeformis* Verity, 1919—042:184—Italy: Toscana.

**monorufopunctata** (if)—*Limenitis anonyma monorufopunctata* Verity, 1950—118:52.

***moritura** (ra)—*Melitaea aurinia moritura* Verity, 1928—068:89—N. Italy: Torino: Venaria Park, M. Musine.

**mundata** (if)—*Melitaea varia mundata* Verity, 1950—118:203—Syntype ♀ [N. Italy: Alpi Marittime].

**nearctica** (ra)—*Boloria pales arsilache nearctica* Verity, 1932—084:104—U.S.A.:

N.E. Alaska—Warren (1944): *Boloria napaea nearctica* [nec Verity], subspecies.

***neclinnaei** (ra)—*Argynnis adippe neclinnaei* Verity, 1936—094:84—Syntypes 8♂♂, 7♀♀ Sweden: Scania: Bokeberg: 23 VII [19]25, 29 VII [19]28, 23 VIII [19]28; [U.S.S.R.]: Lettland: St. Amata: VI, 4-17 VII, VII [????]: Coll. Höfer, Wien.

**NEERAEFORMIS** (ssp)—*Melitaea didyma neeraeformis* Verity, 1915—028: 212—Syntypes 4♂♂, 2♀♀ Italia merid.: Calabria: Aspromonte: 1200 m: 21-25 VII 1914: Querci [leg.]—Original designation uncertain, treated as subspecies by implication; Higgins (1941) considered *neeraeformis* to be an infrasubspecific form of *M. didyma occidentalis* Staudinger, 1901.

***nestonclara** (ra)—*Boloria euphrosyne nestonclara* Verity, 1932—086:112—Syntypes 2♂♂ [Germany]: Berlin.

**nigracastanea** (if)—*Polygonia c-album nigracastanea* Verity, 1950—118:346—Holotype ♂ [Italy]; Firenze: Pian di Mugnone: 7 VI [19]46: Verity [leg.].

**nigriorattenuata** (sf)—*Argynnis lathonia nigriorattenuata* Verity, 1933—088: 58—Syntypes 1♂, 2♀♀ Portugal: Serra da Estrela: 800-1000 m: 2-10 X 1927: Querci [leg.].

***nigroalternans** (ra)—*Melitaea phoebe nigroalternans* Verity, 1919—042:184—[France: Savoie]: Mont Cenis: Bard.

***nigrobscura** (ra)—*Melitaea parthenie nig. obscura* Verity, 1931—083:154—Germany: München: Herrsching.

***nigrogygia** (ra)—*Melitaea phoebe nigrogygia* Verity, 1939—109:17—Syntypes 2♂♂ [Italy]: Istria: Costa Trieste: Venezia Giulia: Abbazia: 15 V 1935.

**nigrolimbata** (if)—*Inachis io nigrolimbata* Verity, 1950—118:360.

**nigroprivata** (sf, ra)—*Argynnis lathonia nigroprivata* Verity, 1933—088:57—Syntypes 2♂♂ France: Gironde: St. Come Bazas: VIII 1918: Sorin [leg.].

**nigroprivataflores** (nomen nudum)—*Issoria lathonia nigroprivataflorens* Verity, 1951—118:pl.49, fig.9—Name for 'synexerge' published in the legend to a figure without description, definition or indication.

***nigrorubida** (ra)—*Melitaea didyma nigrorubida* Verity, 1919—042:180—Syntypes 1♂, 1♀ [Germany]: Sassonia [= Sachsen]: 3 VIII [????].

**nikatorjapygia** (sr)—*Brenthis daphne nikator nikatorjapygia* Verity, 1950—118:267—Italy: Costiera Calabra: Catena, S. Fili: 900 m.

**nitidarubra** (if)—*Boloria napaea napaea nitidarubra* Verity, 1950—118:214—Holotype ♂ [Italy: Südtirol]: Schnalstal: Tirol.

***obscura** (ra)—*Melitaea athalia obscura* Verity, 1919—042:194—Syntypes 6♂♂, 1♀ [Italy: Calabria]: Aspromonte: [illegible]: 12-25 VII 1914.

**obscura** (if)—*Apatura ilia obscura* Verity, 1950—118:24.

***obscuramaxima** (ra)—*Melitaea athalia obscuramaxima* Verity, 1921—042: 213—Syntypes 4♂♂, 2♀♀ Sud Italia: Calabria: Cosenza: San Fili: 900 m: 19 V-25 VI 1920: Querci [leg.].

**occasus** (sf)—*Melitaea didyma mauretanica occasus* Verity, 1919—042:180—N. Africa.

**ochra** (if)—*Melitaea didyma ochra* Verity, 1950—118:104.

***olympena** (ra)—*Argynnis adippe olympena* Verity, 1937—101:21—Syntypes 8♂♂, 2♀♀ [Greece]: Macedonia: Olympus: [850-1700 m]: 16 VI-8 VIII 1935: Romei [leg.]—Brown (1977): *Fabriciana adippe olympena* [nec Verity], subspecies.

***opima** (ra)—*Aglais urticae opima* Verity, 1919—042:199—Syntypes 3♂♂, 1♀ [Italy: Alpi Marittime]: Valdieri: 25 VII [19]09, 14 VII-1 VIII [19]11: Verity [leg.].

***orientalpestris** (ra)—*Melitaea diamina orientalpestris* Verity, 1931—082:81—Syntypes 31♂♂, 10♀♀ [N. Italy]: Alpi Carniche: Sappada: 1300 m: 16 VII-7 VIII [19]26: Verity [leg.].

***orientalpicola** (ra)—*Melitaea athalia orientalpicola* Verity, 1940—113:633—Paratypes 23♂♂, 2♀♀ [N. Italy]: Alpi Carniche: Sappada: 1300 m: 8 VII-7 VIII [19]26: Verity [leg.]; Verity designated holotype and stated that it was collected at 1400 m: probably erroneous statement as all specimens have labels 1300 m only, unless the apparently lost holotype bore different label.

***orientisvivax** (ra)—*Boloria euphrosyne orientisvivax* Verity, 1932—086:121—Syntypes 7♂♂, 3♀♀ [U.S.S.R.]: Burgat. Republ.: Sajan Gbg.: Mondy: Chulugaischa: 3100 m: VII: [ex Bang-Haas].

**PACIFICA** (sp)—*Melitaea pacifica* Verity, 1932—085:71—Holotype ♂, paratypes 3♂♂, 2♀♀ [U.S.S.R.]: Transbaikal mer. occ.: Tschikoi Fluss: Troizkossowsk: 800 m: VII: [ex Bang-Haas]—Higgins (1955) sunk *pacifica* as junior synonym of *Mellicta plotia* (Bremmer, 1861).

***padi** (ra)—*Argynnis hecate padi* Verity, 1933—092:174—Syntypes 4♂♂, 2♀♀ [Italy]: Piemonte: Monte Musine: 27 V [19]12: Satefanelli [leg.]; Emilia: M. Paderno: 11 VI [1]904, 8 VI [1]913: Fiori [leg.]; some specimens with incomplete data.

**padiflorida** (sr)—*Brenthis hecate padi padiflorida* Verity, 1950—118:258—Syntypes 1♂, 2♀♀ [Italy]: Modena: Borzano: 30 VI [19]05; Tana Musine: 1 VII [19]03, 9 VII [19]14; [all] Costantini [leg.].

***padimaxima** (ra)—*Boloria selene padimaxima* Verity, 1933—091:117—Syntypes 3♂♂ [Italy: Modena]; M. Gibbio: [400 m]: 1 V [19]03, 30 IV [19]12: Costantini [leg.]; two specimens with incomplete data.

***padimira** (ra)—*Boloria euphrosyne padimira* Verity, 1932—086:113—Syntypes 3♂♂ [Italy: Modena]; M. Gibbio: [400 m]: 1 V [19]03, 30 IV [19]12: Costantini [leg.]; two specimens with incomplete data.

**paleatincta** (if)—*Melitaea athalia paleatincta* Verity, 1915—028:209—Italy: Monti Sibillini.

***palustris** (ra)—*Melitaea didyma palustris* Verity, 1919—042:181—Syntypes 6♂♂, 2♀♀ [Italy: Toscana]: Antico greto dell'Arno: Marina di Pisa: 26 V 1913: Verity [leg.].

**parthenides** (hy)—*Melitaea parthenides* Verity, 1919—042:194—Syntype ♂ [Italy: Piceno]: Monti Sibillini: Bolognola: [1200 m]: 29 VI-25 VII 1918: Querci [leg.].

***parthenoidemina** (ra)—*Melitaea athalia parthenoidemina* Verity, 1939—109:18—Syntypes 9♂♂, 3♀♀ Greece: Macedonia: Olympus: Prionia: 1500 m, Skala: 300 m; published data confused and probably partly incorrect.

***parvahispanica** (ra)—*Melitaea athalia parvahispanica* Verity, 1940—113:646—Spain: Old Castile: Segovia: San Ildefonso; Aragon: Zaragoza: Veruela.

***parvalpina** (ra)—*Melitaea didyma parvalpina* Verity, 1928—058:163—Syntypes 4♂♂, 3♀♀ [N. Italy]: Alpi Cozie: Clavieres: 1800 m: 29 VII 1925: Verity [leg.].

**parvalpiummixta** (sr)—*Fabriciana adippe alpiummixta parvalpiummixta* Verity, 1950—118:295—Syntypes 10♂♂, 1♀ [N. Italy]: Alpi Cozie: Val Susa: Oulx [= Ulzio]: 1100 m: 14 VII-11 VIII [19]25: Verity [leg.]; Torino: Venaria: 12 VII [19]11, VI 1921, 4 VIII 1937: [Verity], Rocca [leg.]; Torino: Pendici: Monte Musine: Basellette: 4-5 VIII 1937: Rocca [leg.]; [Alpi Marittime]: Valdieri: 29 VII [19]09: [Verity leg.].

***parvanigra** (ra)—*Melitaea athalia parvanigra* Verity, 1940—113:644—Syntypes 5♂♂ Nederland: Byvank: 8-11 VI [19]30, 4 VI [19]31; Scholten [leg.].

***parvavirescens** (ra)—*Argynnis phryxa parvavirescens* Verity, 1929—075:280—Portugal: Serra da Estrela: Querci leg.—Manley & Allcard (1970): *Argynnis adippe paravirescens* [nec Verity], subspecies.

**paulasardonia** (sr)—*Fabriciana elisa elisa paulasardonia* Verity, 1950—118: 281—Syntypes 3♂♂, 1♀ [Italy]: Sardegna: Gennargentu: 15-28 VIII [19]04; Ogliastro: 23 VI [19]04.

**pauper** (sf)—*Melitaea phoebe tusca pauper* Verity, 1919—042:183—Syntypes 2♂♂, 1♀ [Italy]: Modena: M. Gibbio: 1 VIII [19]12; S. Anna P.: 29 VII-4 VIII [19]13; [al] Costantini [leg.].

**phaisanella** (sf)—*Melitaea deione phasanella* Verity, 1950—118:163—N. Italy: Südtirol: Ponte all'Isarco.

**pictior** (if)—*Polygonia c-album pictior* Verity, 1919—042:200—Holotype.S.S.R.]: Gouv. de St. Petersb[urg]; type: *pictior.*

***pinguis** (ra)—*Argynnis niobe pinguis* Verity, 1919—042:196—Syntypes 9♂♂, 8♀♀ [Italy: Alpi Marittime]: Valdieri: VII [18]98, 2-20 VIII 1909: Verity [leg.].

***plena** (ra)—*Melitaea parthenie plena* Verity, 1921—042:213—Syntypes 1♂, 1♀ [France]: H[autes]-Pyr[enees]: Gedre.

**pluriradiata** (if)—*Mesoacidalia charlotta pluriradiata* Verity, 1950—118:301.

***poenina** (ra)—*Melitaea parthenia poenina* Verity, 1931—083:188—Switzerland: Valais: Berisal.

**porrecta** (if)—*Melitaea didyma porrecta* Verity, 1950—118:108.

**postaustrobscura** (sf)—*Melitaea cinxia austrobscura postaustrobscura* Verity, 1950—118:135—Syntypes 7♂♂, 1♀ [France]: A[lpes]-M[aritimes]: St. Barnabe: 11-23 VIII [19]37: Verity [leg.].

**postcarsicola** (sf)—*Melitaea parthenie carsicola postcarsicola* Verity, 1932—083:29—Syntypes 11♂♂, 4♀♀ [Italy]: Costa Trieste: Venezia Giulia: Carso: Opicina: 15 VIII [1]923, 25 VIII [19]26, 5 IX [1]926: Verity [leg.].

**postdia** (sf)—*Boloria dia postdia* Verity, 1933—090:74—Holotype ♂, paratype 1♀ Austria inf[erior]: Krems: 27 VI 1920: Erfurth [leg.].

**postcelladdita** (if)—*Melitaea didyma postcelladdita* Verity, 1950—118:106—Syntypes 1♂, 1♀ [Italy: Abruzzi]: Sirente: Monterotondo: 1500 m: 4 VII [19]41; Gran Sasso: 1400 m: 23 VII 1939: Romei [leg.].

**postfascelis** (sf)—*Melitaea trivia triviafascelis postfascelis* Verity, 1938—109:16—Syntypes 48♂♂, 32♀♀ [Greece]: Macedonia: Olympus: 3500 ft.: 15 VII-VIII 1936: Romei [leg.].

**postgarumma** (sf)—*Melitaea didyma garumma postgarumma* Verity, 1929—069: 72—France: Gironde: Garzac, St. Laurent d'Arce: IX.

**postgentiliana** (sf)—*Boloria selene gentiliana postgentiliana* Verity, 1933—091: 116—Syntypes 14♂♂, 5♀♀ [N. Italy]: Alpi Pennine: [Val Anazasca]: Vanzone: 700 m: 12 VII-1 VIII [19]24, 1-2 IX [19]28: Verity [leg.].

**posticemediocrasse** (if)—*Melitaea didyma posticemediocrasse* Verity, 1950—

118:110—Holotype ♀ [Italy]: Piemonte: Nizza: 13 VIII [????]: Rocci [leg.].

**posticeporrecta** (if)—*Boloria pales palustris posticeporrecta* Verity, 1950—118: 217—Holotype ♂ [N. Italy: Sudtirol: Tirolo: Dolomiti: Pardoi: 1 VIII [1]914: Fiori [leg.].

**postlathonia** (sf)—*Argynnis lathonia postlathonia* Verity, 1933—088:57—Holotype ♂, paratypes 5♂♂, 1♀; holotype [Nederland]; Hilversum: 21 VII 1901: [illegible]; paratypes [Germany]: Cassel [= Kassel]; [England]: Canterbury: 1906: [illegible].

**postluciflua** (sf, if)—*Melitaea athalia luciflua postluciflua* Verity, 1940—113: 620—Syntypes 2♂♂ [Switzerland]: Geneve: 15 VIII 1916, 16 VIII 1915: Perinet [leg.].

**postmelida** (sf)—*Melitaea athalia melida postmelida* Verity, 1940—113:622—[Italy/Switzerland]: Monte Generoso.

**postmelangraphata** (sf, if)—*Melitaea athalia helvetica melangraphata posstmelangraphata* Verity, 1940—113:622—Syntypes 2♂♂, 1♀ [N. Italy]: Alpi Pennine: [Valle Anzasca]: Vanzone: 700 m: 19 VIII-2 IX [19]28: Verity [leg.].

**postnaina** (sf)—*Melitaea didyma naina naina postnaina* Verity, 1950—118:125—Syntypes 3♀♀ [Italy]: Südtirol: [Valle Isarco]: VIII 1918.

**postnarenta** (sf)—*Melitaea phoebe narenta postnarenta* Verity, 1939—109:17—Greece: Macedonia: S. Dionisio: 800 m: 17-18 VIII.

**postogygia** (sf)—*Melitaea phoebe ogygia postogygia* Verity, 1938—109:16—Syntypes 2♂♂, 1♀ [Greece]: Macedonia: Salonica [= Thessaloniki]: 1000 ft.: 12-13 VIII 1936; Olympus: 2500 ft.: 17 VIII 1935; [all] Romei [leg.].

**postpadimaxima** (sf)—*Clossiana selene padimaxima postpadimaxima* Verity, 1950—118:234—Syntypes 5♂♂ [Italy: Milano]: Turbigo: [146 m]: 27 VII [19]30: Rocci [leg.].

**postoreithyia** (sf)—*Melitaea didyma oreithyia postoreithyia* Verity, 1929—069: 91—Italy: Trieste.

**postsubluciflua** (sf)—*Melitaea athalia subluciflua postsubluciflua* Verity, 1940—113:620—Syntypes 10♂♂, 2♀♀ [France]: A[lpes]-M[aritimes]: Vence: 20 VIII [19]37: Verity [leg.].

**posttarlonia** (sf)—*Melitaea didyma tarlonia tarlonia posttarlonia* Verity, 1950—118:126—Syntypes 2♂♂ [N. Italy]: Alpi Pennine: [Valle Anzasca]: Vanzone: 700 m: 18-26 VIII [19]28: Verity [leg.].

**postvirgilia** (sf)—*Melitaea phoebe virgilia postvirgilia* Verity, 1950—118:154—Syntypes 4♂♂, 1♀ [France]: A[lpes]-M[aritimes]: Vence: 20-30 VIII [19]37: Verity [leg.].

**postvividior** (sf)—*Melitaea athalia vividior postvividior* Verity, 1930—078:132—Syntypes 3♂♂ [Switzerland]: Bellinzona: Reazzino: [230 m]: 3 VII [19]07.

**postwheeleri** (sf)—*Melitaea dictynna wheeleri postwheeleri* Verity, 1930—07: 109—Syntypes 3♂♂ [Switzerland]: Bellinzona: Reazzino: [230 m]: 3 VII [19]07.

**praemarsilia** (ra, sf)—*Melitaea didyma praemarsilia* Verity, 1929—069:74—Syntypes 7♂♂, 1♀ [N. Italy]: Lago Maggiore: Intra: Pian Quaggie: 950 m: 18-21 VI 1922: Verity [leg.]; original rank and distribution uncertain, further 9♂♂, 1♀ from France: Lozere, Aveyron and Bulgaria: Lulin could possibly belong to the type-series.

***praenikator** (ra)—*Argynnis daphne praenikator* Verity, 1933—087:107—Syntypes 13♂♂, 7♀♀ [Italy]: Südtirol: [Klausen]: 523 m: VI 1918; some specimens with incomplete data.

**praestantior** (sf, if)—*Melitaea deione praestantior* Verity, 1932—087:141—S. France Var: St. Baume.

**primigenia** (sf)—*Limenitis rivularis primigenia* Verity, 1924—052:35—Syntypes 1♂, 1♀ Italia centrale: Toscana: Firenze: Fosse Vignore: 100 m: 12 V 1919; Firenze: Petraia: 21 V [19]20; Verity, Querci [leg.].

**PROTEA** (ssp)—*Melitaea didyma protea* Verity, 1917—034:183—Syntypes 50♂♂, 25♀♀ [Italy: Toscana: Firenze]: Pian di Mugnone: 200 m: 16 V-2 VII 1915: [Querci leg.]; 'seria tipica', 'copipi': *protea*; part of original type-series destroyed and/or lost; all specimens remounted and relabelled; Verity gave also 'Poggio' as type-locality, but no specimens from Poggio found in the type-series—Original rank uncertain, treated therefore as subspecies by implication—Higgins (1941) sunk *portea* (by implication: treated as infrasubspecific form) as junior synonym of *Melitaea didyma occidentalis* Staudinger, 1861.

***proteaoccidentis** (ra)—*Melitaea didyma proteaoccidentis* Verity, 1929—069: 117—Syntypes 2♂♂, 1♀ Morocco: Meknes: [Middle Atlas Mts.]: Foum Kheneg: VII 1920.

**pseudocleodoxa** (if)—*Argynnis phryxa pseudocleodoxa* Verity, 1929—075:278.

**pseudodelminia** (if)—*Melitaea athalia delminia psseudodelminia* Verity, 1940—113:627.

**pseudoiris** (nomen nudum)—*Apatura pseudoiris* Verity, 1913—023:181—Replacement name for species *Apatura iris* of all authors but Linnaeus, published without description, definition or indication.

***pulchrior** (ra)—*Vanessa polychloros pulchrior* Verity, 1916—033:101—Syntype ♀ [Italy: Toscana]: Firenze: ex larva; type: *pulchrior.*

**pumila** (if)—*Melitaea didyma pumila* Verity, 1919—042:181.

**punctifera** (if)—*Melitaea athalia punctifera* Verity, 1915—028:209—Italy: Piceno.

***pygmaena** (ra)—*Limenitis rivularis pygmaena* Verity, 1928—058:143—Syntypes 5♂♂, 1♀ [Italy]: Toscana: Livorno: Quercianella: 11-27 VIII [19]22; Livorno: Limone: 8 VI 1917; [all] Verity [leg.].

***pyrenaealpestris** (ra)—*Melitaea diaminia pyrenaealpestris* Verity, 1931—082: 70—Syntypes 7♂♂, 3♀♀ [France: Hautes-Pyrenees]: Gedre: 9-15 VI [19]16: Rondou [leg.]; some specimens with incomplete data.

***pyrenaealpina** (ra)—*Melitaea didyma pyrenaealpina* Verity, 1929—069:73—Syntypes 6♂♂, 9♀♀ [France]: H[autes]-P[yrenees]: Gedre: VI [19]15, VII [19]16, 10 VII [19]19: Rondou [leg.].

***pyrenemiscens** (ra)—*Boloria pales pyrenemiscens* Verity, 1932—084:102—France: Hautes-Pyrenees: Gedre—Raised to subspecies-rank and redescribed: *Boloria pales pyrenemiscens* Warren, 1944.

***pyrenesdebilis** (ra)—*Melitaea aurinia pyrenesdebilis* Verity, 1928—068:90—Syntype ♂ [France]: Pyr[enees]-Or[ientales]: Porte [de Puymorens]: 16 VII [19]25: Col. Stempffer; type—Manley & Allcard (1970): *Euphydryas aurinia pyrenesdebilis* [nec Verity], subspecies.

**radiata** (if)—*Argynnis daphne nikator radiata* Turati & Verity, 1911—015:212—Holotype ♀ [N. Italy: Alpi Marittime]: Valdieri: 20 VIII 1909: Verity [leg.]; type: *radiata*.

***ravalpina** (ra)—*Melitaea didyma ravalpina* Verity, 1929—069:90—Syntypess 3♂♂, 2♀♀ [N. Italy]: [Süd]tirol: Schnalstal: [800 m]: [4 VII 1920]: Astfäller [leg.].

***rectealpina** (ra)—*Melitaea didyma rectealpina* Verity, 1929—069:66—Syntypes 14♂♂, 12♀♀ [N. Italy]: Alpi Retiche: Bormio: 1300 m: 1-11 VIII [19]27: Verity [leg.].

**relevata** (if)—*Argyronome paphia relevata* Verity, 1934—093:79—Syntypes 1♂, 1♀ [France]: Bass[es]-Alp[es]: Digne: Morderique Tal: Mitte VII 1931: Rütimeyer, Bern [leg.].

**romula** (sf)—*Melitaea didyma romana romula* Verity, 1922—042:12—Syntypes 8♂♂, 4♀♀ [Italy]: Roma: Genzano: VIII 1921.

**romulanigra** (sf)—*Melitaea didyma patycosana romulanigra* Verity, 1950—118: 115—Syntypes 2♂♂, 18♀♀ [Italy]: Lazio: Roma: 100 m: [Verano]: 15-18 X 1939: Romei [leg.].

***rubens** (ra)—*Eugonia polychloros rubens* Verity, 1919—042:199—Holotype ♂ [Italy]: Sardegna: [Lanusei]; type: *rubens*.

**rubescens** (if)—*Charaxes jasius rubescens* Verity, 1950—118:18.

**RUBIDA** (ssp)—*Argynnis niobe rubida* Verity, 1915—028:214—Syntypes 3♂ Italia merid.: Calabria: Aspromonte: [Rovescio: Pian di Carmelia]: 1200 m: 10-12 VII 1914: Querci [leg.].

**rubida** (sf)—*Melitaea didyma rubida* Verity, 1919—042:179—France: Paris.

**rubidaprotea** (sr)—*Melitaea didyma marsilia rubidaprotea* Verity, 1950—118: 122—Syntypes 1♂, 1♀ [S. France]: Saint Baume: Plan d'Aups: 800 m: 2 V 1936: Foulquier legit; Nans: 27 V 1934.

***rubidior** (ra)—*Argynnis aglaja rubidior* Verity, 1935—095:190—Syntypes 4♂♂ [N. Italy]: Lago Maggiore: Intra: Pian Quaggie: 950 m: 20 VI 1922; Mottarone: 1450 m: 18 VII [19]22; [all] Verity [leg.].

**rubrofusca** (if)—*Issoria lathonia lathonia rubrofusca* Verity, 1950—118:271—Syntypes 3♂♂ [N. Italy]: Alpi Carniche: S. Stefano [di Cadore]: 900 m: 16 VII [19]26; Italia centrale: Firenze: Pian di Mugnone: 200 m: 11 IV 1916; Fosso Gamberaia: 200 m: 17 IV 1916; Verity, Querci [leg.].

**rufoanulata** (if)—*Limenitis camilla rufoanulata* Verity, 1950—118:46.

**sardonia** (sr)—*Fabriciana elisa sardonia* Verity, 1950—118:281—Syntypes 3♂♂, 3♀♀ [Italy]: Sardegna: Cagliari.

***sayanskalpina** (ra)—*Melitaea ambigua sayanskalpina* Verity, 1940—113:600—Holotype ♀, paratypes 11♂♂, 2♀♀ [U.S.S.R.]: Gouv. Irkutsk: Mondy: Sajan mont. or. Chulugaischa: 2600 m: VI; Tunkische Weisberge: Turan: 2000 m: VII; [all ex Bang-Haas].

***semiclarens** (ra)—*Argynnis adippe semiclarens* Verity, 1936—094:85—Syntypes 1♂, 1♀ [France]: Hospitalet: 800 m: 8 VII [19]28; Obs. Aigoual: 16 VIII [19]25; [both] Gaillard [leg.]; original rank uncertain, presumably race or transitional form.

***semiplena** (ra)—*Melitaea parthenoides semiplena* Verity, 1931—083:140—Syntypes 2♂♂, 1♀ [S. France]: Cevennes: Mt. Aigoual: 12 VI 1927; La Sereyrede: 12 VI 1927; [all] Gaillard [leg.].

***septentrionalis** (ra)—*Charaxes jason septentrionalis* Verity, 1913—023:180—Syntypes 2♂♂, 1♀ [Italy: Toscana: Lucca]: Forte dei Marmi: 10 IX [1]904, 20 IX [1]901: [Verity leg.].

**SEPTENTRIORIENTIS** (nn)—*Melitaea septentriorientis* Verity, 1930—078: 74—Replacement name for *Melitaea parthenie orientalis* Menetries, 1859, said to be invalid junior homonynm of *Melitaea orientalis* Herrich-Schaffer, 1847; there was no need for Verity's action as the preoccupied name was replaced earlier by *Melitaea parthenie menetriesi* Caradja, 1895.

**septiespupillata** (nomen nudum)—*Pyrameis atalanta septiespupillata* Verity 1919—042:198—Name for individual form published without description, definition or indication.

**septiespupillata** (if)—*Vanessa atalanta septiespupillata* Verity, 1950—118:336—Holotype ♂ [Italy]: Spezia: Pertusola: 21 VIII [19]13: Verity [leg.]; type: *septiespupillata.*

**septiespupillata** (if)—*Pyrameis cardui septiespupillata* Verity, 1919—042:198—Holotype ♀ Italia centrale: Toscana: Palazzuolo Romagna: 700 m: 16 VIII 1917: Querci [leg.].

**sesquiargentea** (if)—*Euphydryas aurinia sesquiargentea* Verity, 1950—118:72.

***sesquierilda** (ra)—*Brenthis ino sessquierilda* Verity, 1952—116:385—Syntypes 1♂, 2♀♀ [France]: Pyr[enees]-Or[ientale]: Porte [de Puymornes]: 6 VII [19]30, 3-10 VII [19]31: [Deslandes leg.].

**sexiespupillata** (if)—*Pyrameis cardui sexiespupillata* Verity, 1919—042:198—Holotype ♀ [Italy: Firenze]: Vallmbrosa: VIII 1905: Verity [leg.].

**sexiespupillata** (nomen nudum)—*Pyrameis atalanta sexiespupillata* Verity, 1919—042:198—Name for individual form published without description, definition or indication.

**sexiespupillata** (if)—*Vanessa atalanta sexiespupillata* Verity, 1950—118:336—Holotype ♂ [Italy]: Firenze: 4 VI [19]18: ex larva; type: *sexiespupillata.*

**siccalta** (ra, sr, sf)—*Melitaea didyma romana siccalta* Verity, 1950—118:116—Syntypes 4♂♂, 10♀♀ [Italy]: Abruzzi: Gran Sasso: 1400 m: 18-25 VII 1939; Sirente: Monterotondo: 1400 m: 19 VII-17 VIII [19]41; [all] Romei [leg.].

***siciliaena** (ra)—*Argynnis daphne siciliaena* Verity, 1933—087:107—Syntypes 4♂♂, 2♀♀ [Italy: Sicily]: Madonie: VII 1929; Madona dell'Alto: VII 1929; M[onte] S. Salvatore: VII 1929; [all Mariani leg.].

**siculapinguis** (sr)—*Melitaea athalia sicula siculapinguis* Verity, 1950—118:176—Syntypes 7♂♂ [Italy: Sicily]: Messina: Zappula: 1 VI [19]33, 25 VI [19]33, 9 VI [19]34, 22 VI [19]34.

***strandi** (ra)—*Aglais urticae strandi* Verity, 1936—100:481—Syntypes 3♂♂ [France: Vendee]: Puybilliard: 6 VII [????].

***stricta** (ra)—*Argynnis hecate stricta* Verity, 1933—092:175—Syntype ♂ France: Bass[es]-Alpes: Montagne de Lures: 23 VII 1931: Rütimeyer [leg.].

***strigosa** (ra)—*Argynnis hecate strigosa* Verity, 1933—092:175—Syntypes 2♂♂ [France]: Lot: Cabreret: 8 VI 1926.

***subalpina** (ra)—*Melitaea didyma subalpina* Verity, 1919—042:180—Syntypes 2♂♂, 1♀ [Italy: Torino: Alpi Cozie]: Val Susa: Bussoleno: Falcimagna: 850 m: VIII:

[illegible].

**subcorythalia** (sf)—*Melitaea phoebe occitanica subcorythalia* Verity, 1928—058: 162—Syntypes 4♂♂, 2♀♀ [France]: Vendee: Auzay: 3 VIII 1901, 16 VIII 1920, 20 VIII 1918: Lucas [leg.].

***subhelvetica** (ra)—*Melitaea athalia helvetica subhelvetica* Verity, 1935—094: 74—Syntypes 8♂♂ [Switzerland]: Valais: Martigny: La Batiax: 2 VI 1927, 10-31 VII [19]32, 28 VI-10 VII [19]33: Verity [leg.]; some specimens probably not from La Batiaz.

**subluciflua** (ra)—*Melitaea athalia helvetica subliciflua* Verity, 1935—094:74—Syntypes 8♂♂ [Switzerland]: Valais: Martigny: La Batiaz: 2 VI 1927, 10-30 VII [19]3, 28 VI-10 VII [19]33: Verity [leg.]; not all specimens labelled La Batiaz.

***submaxima** (ra)—*Melitaea athalia submaxima* Verity, 1924—052:40—Syntypes 11♂♂, 3♀♀ [Italy]: Toscana: Lucca: Forte dei Marmi: 3-6 VII [19]13, 10 VII [1]907, 8-24 VII 1923; [some] Querci [leg.].

**suboccitanica** (ra, sf)—*Melitaea phoebe suboccitanica* Verity, 1928—058:162—Syntype 1♂ [France]: V[end]ee: Auzay: 1 VI 1917; rest of type-series probably lost or destroyed.

***subpatycosana** (ra)—*Melitaea didyma subpatycosana* Verity, 1924—054:38—Syntypes 10♂♂, 10♀♀ Italia centr.: Lucca: Valle Camayone: 300 m: 10-18 VII 1923: Querci [leg.].

***subrubida** (ra)—*Melitaea didyma subrubida* Verity, 1919—042:180—Syntype 1♂ [Germany: Berlin]; type; rest of type-series (at least further two specimens) probably destroyed by museum pests.

**subrubidaprotea** (sr)—*Melitaea didyma marsilia subrubidaprotea* Verity, 1950—118:122—Syntypes 1♂, 4♀♀ [France: Alpes-Maritimes]: Var: Nice: Levens, Falicon: 30 VI [19]39, 2-4 VII 1929, 21 VII [19]39; [some] Coll. Rütimeyer; some specimens with incomplete data.

***subseilemis** (ra)—*Melitaea didyma subseilemis* Verity, 1929—069:73—Syntypes 2♂♂, 2♀♀ [France]: Cevennes: Concoules: Mt. Lozere: 6 VII [19]24, 4 VII [19]26; Mt. Aigoual: 3 VIII [19]20; Gaillard, Foulquier [leg.].

***subtarlonia** (ra)—*Melitaea didyma subtarlonia* Verity, 1929—069:74—Syntypes 13♂♂, 7♀♀ [N. Italy]: Lago Maggiore: Intra: Pian Quaggie: 950 m: 6-7 VI 1922: Verity [leg.].

***subtusca** (ra)—*Melitaea phoebe subtusca* Verity, 1952—116:349—Syntypes 4♂♂, 3♀♀ [France: Var]: Ste. Baume: Nans[-les-Pins]: [300 m]: 24 V [19]26, 7 V [19]30, 23 V [19]33, 24 V 1936: Foulquier [leg.].

***subvitatha** (ra)—*Argynnis aglaja subvitatha* Verity, 1935—095:202—Syntypes 4♂♂ [W. China]: Tianschan: Aksutal: Sary-dshasy mont.: 2000 m: VII: [ex Bang-Haas].

***superalpina** (ra)—*Melitaea didyma superalpina* Verity, 1929—069:66—Syntypes 1♂, 1♀ [N. Italy]: Alpi Retiche: Bormio: Val di Fraele: 2000 m.

**suprapupillata** (if)—*Proclossiana eunomia suprapupillata* Verity, 1950—118:226.

***synexergica** (ra)—*Melitaea athalia synexergica* Verity, 1930—078:133—Switzerland: Bernese Oberland: isenfluh; Canton Seleure: Jura.

***tenuicula** (ra)—*Melitaea athalia tenuicula* Verity, 1919—042:193—Syntypes

40♂♂, 35♀♀ [Italy: Piceno]: Monti Sibillini: Bolognola: [1200 m]: 29 VI-25 VII 1918: [Querci leg.]; all specimens remounted and relabelled—Original rank: 'somation' of a race.

***tenuitermaculosa** (ra)—*Brenthis daphne tenuitermaculosa* Verity, 1922—042: 14—Syntypes 6♂♂, 5♀♀ Italia centrale: Firenze: Pian di Mugnone: 200 m: 13-21 VI 1915; Certosa: 5 VII [19]18; Colline di Firenze: 400 m: 23 VI-26 VII 1914; Querci, Verity [leg.].

***tenuis** (ra)—*Melitaea athalia tenuis* Verity, 1919—042:193—Syntypes 48♂♂, 12♀♀ [Italy]: Firenze: [Fiesole]: Pian di Mugnone: 13 VI-12 VII 1915: [Querci leg.].

**translucens** (if)—*Melitaea aurinia glaciegenita translucens* Verity, 1928—068:48—Syntype ♂ [N. Italy]: Südtirol: 19[??]; type: We[illegible].

***triviafascelis** (ra)—*Melitaea trivia triviafascelis* Verity, 1937—101:18—Syntypes 40♂♂, 16♀♀ [Greece]: Macedonia: Salonika [= Thessaloniki]: 1000 ft.: V 1935: Romei [leg.].

***tusca** (ra)—*Melitaea phoebe tusca* Verity, 1919—042:183—Syntypes 1♂, 2♀♀ [Italy]: Toscana: Firenze: [illegible]: 17 VI [19]04, 9 V [19]13: Verity [leg.].

**uncumminans** (if)—*Melitaea athalia helvetica uncumminans* Verity, 1940—113: 612—Italy: Milano: Turbigo.

***universa** (ra)—*Pyrameis cardui universa* Verity, 1919—042:197—Syntype 1♂ [Italy]: Firenze: IV [19]08: [Verity leg.].

***ussuriae** (ra)—*Melitaea pacifica ussuriae* Verity, 1932—085:72—Syntypes 9♂♂, 4♀♀ [U.S.S.R.]: Ussuri: Wladiwostock Occ.: Sutschanski-Rudnik: VII: [ex Bang-Haas].

***variabella** (ra)—*Melitaea varia varabella* Verity, 1931—083:152—Syntypes 1♂, 2♀♀ [Italy]: Alpi Marittime: Vallasco: VIII 1904; some specimens with incomplete data.

***varianana** (ra)—*Boloria euphrosyne varianana* Verity, 1932—086:114—Syntypes 3♂♂ [England]: Durham: Birtley: 24 V-VI [1]902: ex larva.

***varissima** (ra)—*Melitaea varia varissima* Verity, 1915—028:210—Italy: Piceno: Monti Sibillini: Bolognola: Piano Astore: 1200-1600m.

**veragrorum** (ra)—*Melitaea athalia helvetica veragrorum* Verity, 1935—094:74—Switzerland: Martigny: Bex: damp meadows: VI-VII.

***vesubiana** (ra)—*Melitaea deione vesubiana* Verity, 1932—087:141—Syntypes 1♂, 4♀♀ [France]: Gallia mer.: St. Martin-Ves[ubie]: VI [19]29: Coll. Höfer, Wien.

**vesubiella** (sf)—*Melitaea deione vesubiana vesubiella* Verity, 1932—087:141—Syntypes 3♂♂, 3♀♀ [France]: Gallia mer.: St. Martin-Ves[ubie]: 10-21 VIII [19]29: Coll. Höfer, Wien.

**violascens** (if)—*Limenitis anonyma violascens* Verity, 1950—118:52.

**viridescens** (if)—*Limenitis anonyma viridescens* Verity, 1950—118:52.

***vividicolore** (ra)—*Melitaea parthenie vividicolore* Verity, 1931—083:186—Holotype ♂ Ungheria [= Hungary]: Kisnyir.

***vulgoadippe** (ra)—*Argynnis phryxa vulgoadippe* Verity, 1929—075:279—Paratypes 2♂♂ [England]: Hampshire: [Southampton]: New Forest: 7 VII 1928: EMG & PPG [leg.]; holotype apparently destroyed with the rest of type-material by museum pests.

## SATYRIDAE

***abetonica** (ra)—*Erebia ceto abetonica* Verity, 1919—042:124—Syntypes 1♂, 1♀ [Italy: Toscana]: Abetone: [Monte Majori: Passo Abetone: 1500 m]: 9 VII [19]12.

**adrastaeformis** (if)—*Pararge maera vulgaris appennina adrastaeformis* Verity, 1919—042:127—Syntype ♀ Italia centrale: Piceno: Massicchio Sibillini: Bolognola: 1600 m: 18 VII 1918: Querci [leg.].

**albapennina** (sr)—*Hiparchia statilinus apennina albapennina* Verity, 1953—120:333—Syntype ♂ [Italy]: Abruzzi: Gran Sasso: 1300-1400 m: 10 VIII 1939: Romei [leg.]; rest of type-series destroyed by museum pests.

**albolimbo** (if)—*Hyponephele lycaon analampra albolimbo* Verity, 1953—120: 242—Holotype ♂ [Italy]: Marche: Bolognola: 7 VII 1937: Querci [leg.]; 'olotipo': *albolimbo.*

**albovittata** (if)—*Erebia neoridas etrusca albovittata* Verity, 1904—004:55—Syntypes 2♀♀ [Italy: Toscana]: Alpi Apuane: Mt. Matana: VIII [19]01, VIII [1]903: [Verity leg.].

***alcyoneformis** (ra)—*Satyrus hermione alcyoneformis* Verity, 1911—017:312—Syntypes 4♂♂ [Italy: Toscana: Firenze]: Vallombrosa: VIII 1905; Pistoiese: Pisazorna: [all Verity leg.].

**altera** (if, sf)—*Coenonympha corinna elbana altera* Verity, 1917—034:192—Italy: Isola d'Elba.

***alticola** (ra)—*Pararge megaera alticola* Verity, 1911—016:269—Syntype ♀ [Italy: Alpi Maritiime]: Valdieri: [1375 m]: 1 VIII [19]11: [Verity leg.]; rest of type-series apparently lost or destroyed.

**ALTIVOLANS** (nn)—*Erebia meolans altivolans* Verity, 1935—094:57—Replacement name for *Papilio irene* Hübner, 1805, which is primary junior homonym of *Papilio irene* Drury, 1782; Verity gave the authorship of the senior homonym erroneously to Linnaeus; according to Warren (1936), *altivolans* is junior subjective synonym of *Papilio stygne* Ochsenheimer, 1807.

***amplevittata** (ra)—*Erebia epiphron amplevittata* Verity, 1921—042:211—Syntypes9♂♂, 4♀♀ Italia centrale: Toscana: Alpi Apuane: Sumbra: 1200 m: 14 VI-20 VII 1920: Querci [leg.]; [Italy: Modena: Alpe delle] Tre Potenze: 23 VII [19]12: Costnatini [leg.]; [Italy: Modena]: Foce a Giovo: [1674 m]: 23 VII [19]12: Costantini [leg.].

***angliae** (ra)—*Hipparchia semele angliae* Verity, 1924—051:22—Great Britain.

***anglorum** (ra)—*Hipparchia semele anglorum* Verity, 1924—051:22—Great Britain.

**anommata** (if)—*Epinephele jurtina anommata* Verity, 1904—004:56—Holotype ♂ [Italy]: Firenze: Monte Senario: 1 VII [1]903: [Verity leg.]; type: *anommata.*

**anteappennina** (nn)—*Satyrus maera anteappennina* Verity, 1927—058:156—Replacement name for infrasubspecific unavailable name *Pararge maera vulgaris* Verity, 1913 said to be preoccupied by available subspecies-rank name *Hipparchia egeria vulgaris* Zeller, 1847. These taxa are not considered congeneric at present.

**antelatecana** (sf)—*Coenonympha pamphilus latecana antelatecana* Verity, 1953—120:120—Holotype ♂, Paratypes 3♂♂, 1♀ [France: Alpes-Maritimes: Nice]: Vence: 18 IV [19]28, 20 IV [19]35: Gazel [leg.]; Brock: [700-800 m]: 16 VII [19]35: Verity [leg.]; Passanglia: 13 VI [19]31: Gazel [leg.].

**antelyllus** (sf, if)—*Coenonympha pamphilus lyllus antelyllus* Verity, 1926—057: 197—Holotype ♂ [Spain]: Cordova: 11 IV 1901: Coll. Yerbury: 1901-144: [ex BM(NH)].

**anteorientalis** (sf)—*Lasiommata maera orientalis anteorientalis* Verity 1938—108:10—Syntypes 1♂, 1♀ [Turkey]: Asia Minor c.: Ak-Chehir: 23 V; Sultan Dagh: 1700 m: 20 V [19]30: [both] Coll. Wagner, Wien.

**anteparvorientalis** (nomen nudum)—*Lasiommata maera parvorientalis anteparvorientalis* Verity, 1938—108:11—Name for seasonal form published without description, definition or indication.

***antevortes** (ra)—*Erebia philomela antevortes* Verity, 1927—064:173—Syntypes 2♂♂ [France]: Pyrenees: Cauterets: 11 VII [19]24—Warren (1936): *Erebia euryale antevortes* [nec Verity], subspecies.

**antherosenthes** (nomen nudum)—*Hipparchia semele antherosenthes* Verity, 1953—119:175—Name for race published 31 VII 1953 without description or definition, with indication to work unpublished at the time (Kudrna 1977).

**antherosenthes** (sr)—*Hipparchia semele senthes antherosenthes* Verity, 1953—120:305—[Greece]: Macedonia: Olympos: Skala—Published 31 XII 1953 (Kudrna 1977).

**anulata** (if)—*Agapetes russiae russiae japygia anulata* Verity, 1953—120:59—Holotype (♂) [Italy]: Gran Sasso: 1300-1700 m: 8 VII 1939: Romei [leg.].

**appennina** (ra, sr, if)—*Pararge maera appennina* Verity, 1911—016:269—Syntypes 8♂♂, 4♀♀ [Italy: Toscana]: Appennino Pistoiese: [illegible]: 20 VIII-3 IX [19]11: [Verity leg.]—Original rank uncertain, confused, probably infrasubspecific, as Verity (042:127) confirmed in 1919.

***apenninicola** (ra)—*Erebia euryale apenninicola* Verity, 1911—017:312—Syntypes 1♂, 3♀♀ [Italy: Toscana]: Appennino Pistoiese: Il Teso, Abetone, San Marcello: 12 VIII [18]99, VIII [1]901: [Verity leg.].

***apenninigena** (ra)—*Hipparchia semele apenninigena* Verity, 1923—051:156—Syntypes 2♂♂, 1♀ Italia centr.: Piceno: Bolognola: Massicchio Sibillini: 1200-1700 m: 14-30 VII 1918, 22 IX 1919: Querci [leg.].

***apenninigena** (ra)—*Erebia goante apenninigena* Verity, 1919—042:124—[Italy]: Ligurian Alps: Arpetto.

**apicalis** (if)—*Coenonympha arcania macromma apicalis* Turati & Verity, 1911—015:238—Holotype ♂ [Italy]: Alpi Marittime: Valdieri: VIII [18]98; type: *apicalis.*

***apuana** (ra)—*Erebia aethiops apuana* Verity, 1923—049:135—[Italy]: Alpi Apuane: Acqua Bianca: 1300 m; Mt. Pisarino: 11 VI 1920.

**apupillata** (if)—*Satyrus statilinus allionia apupillata* Verity, 1917—034:190—Italy: Isola d'Elba.

**arenosa** (sf)—*Coenonympha pamphilus latevittata arenosa* Verity, 1926—057: 198—Syntype ♂ [Morocco: Middle Atlas]: Fez: 20 V 1920; type: *arenosa.*

***asiaemontium** (ra)—*Coenonympha pamphilus asiaemontium* Verity, 1926—057:206—Syntypes 7♂♂, 3♀♀ [U.S.S.R.]: Alai centr. mont.

**astriata** (if)—*Satyrus statilinus allionia astriata* Verity, 1917—034:190—Syntype ♂ [Italy]: Toscana: [Lucca]: Forte dei Marmi; *astriata.*

**atavica** (if)—*Pararge aegeria egerides intermedia atavica* Verity, 1919—042:127—

Syntype ♀ Italia centr.: Toscana: Firenze: Parco Caserne: 50 m: 6 IV 1919: Querci [leg.].

***atlantea** (ra)—*Coenonympha pamphilus atlantea* Verity, 1926—057:199—N. Africa: Atlas Mts.: in valleys—Rank uncertain, possibly intended for infrasubspecific form.

**ATLANTEA** (nn)—*Nytha actaea atlantea* Verity, 1927—064:174—Replacement name for *Satyrus actaea maroccana* Lucas, 1920, said to be preoccupied by *Satyrus mniszechi maroccana* Meade-Waldo, 1905.

**AUSTRALIS** (ssp)—*Coenonympha pamphilus australis* Verity, 1915—028:227—Italy: Piceno: Colli di Macerata: 300 m: 24 IX 1913; Toscana: Firenze: 9 V 1913; Toscana: Lago di Porta de la Versilia: 30 VIII 1914—Type-material apparently lost or detroyed by museum pests; Davenport (1941) recognized *australis* at subspecies rank and restricted by implication the type-locality to 'hills of Macerata'.

**barcionis** (ra, sf)—*Coenonympha pamphilus barcionis* Verity, 1926—057:203—Syntype ♂ [Spain]: Catalonia: Llinas: 200 m: 28 V [19]25: Querci [leg.]; specimen consists of wings glued to a card, rest of type-series probably destroyed by museum pests—Manley & Allcard (1970): *Coenonympha pamphilus barcionis* [nec Verity], subspecies.

**basilineola** (if)—*Agapetes psyche pherusa basilineola* Verity, 1953—120:54—Syntype ♂ [Italy: Sicily: S. Martino: V].

**basilineola** (if)—*Agapetes russiae japygia basilineola* Verity, 1953—120:59—Syntype ♀ [Italy]: Lazio: Monte Meta: Fonte Larocca: 1000 m: 2 VIII [19]40.

***bellorum** (ra)—*Nytha actaea bellorum* Verity, 1927—064:174—Syntypes 5♂♂ [Spain]: Nueva Castilla: Cuenca: Huelamo: 1200 m: 10-31 VII 1926: Querci [leg.]—Manley & Allcard (1970): *Satyrus actaea bellorum* [nec Verity], subspecies.

**biantepupillata** (if)—*Satyrus statilinus allionia biantepupillata* Verity, 1917—034:190—Italy: Isola d'Elba.

**bicubitocellata** (nn)—*Pararge aegeria bicubitocellata* Verity, 1953—120:24—Replacement name for an aberration-name said to be preoccupied.

**bicuneata** (if)—*Melanargia galathea turcica bicuneata* Verity, 1914—028:216—Italy: Aspromonte: Pian di Carmelia: 25 VII 1914.

**bilinea** (if)—*Pararge aegeria vulgaris bilinea* Verity, 1953—120:13—Syntype ♀ [Italy: Toscana]: Firenze: Via Leone X: 30 III [19]11.

**bipertita** (if)—*Coenonympha pamphilus emiaustralis bipertita* Verity, 1919—042:121—Holotype ♀ [Switzerland]: Vellese: Wulfschlegel [leg.]; type: *bipertita.*

**bipicta** (if)—*Satyrus semele scota bipicta* Verity, 1916—033:165—Syntype ♀ [England]; type: *bipicta.*

**BRITANNIAE** (ssp)—*Epinephele tithonus britanniae* Verity, 1915—028:220—Syntypes 13♂♂, 10♀♀ [Enland: Cornwall]: Bude: 15-19 VII 1894; Benfleet: 17 VII [18]98, 2 VIII [18]99: [all] Conquest [leg.].

***burdigalae** (ra)—*Satyrus statilinus burdigalae* Verity, 1919—042:128—Syntypes 1♂, 1♀ France: Bordeaux; type: *burdigalae.*

**caeca** (if)—*Erebia gorge gorge caeca* Verity, 1953—120:167—Syntype ♂ [N. Italy]: Alpi Carniche: Sappada: Passo Houbolt: 2300 m.

***calabra** (ra)—*Melanargia galathea calabra* Verity, 1915—028:215—Syntypes

11♂♂, 15♀♀ [Italy]: Calabria: [Aspromonte]: Altipiani di Carmelia: [700-1200 m]: 12-25 VII 1914: Querci [leg.]; all remounted and relabelled.

***calabraprocida** (ra)—*Melanargia galathea calabraprocida* Verity, 1921—042: 212—Syntypes 7♀♀ [Italy]: Calabria: Catena: Cocenza: San Fili: 900 m: 1-21 VI 1920: Querci [leg.].

***caledonia** (ra)—*Pararge megaera caledonia* Verity, 1911—017:314—Syntypes 3♂♂ Scozia [= Scotland]: Costa settent.: 8 VIII [????].

***caledonia** (ra)—*Erebia aethiops caledonia* Verity, 1911—017:311—Syntypes 4♂♂ Scozia [= Scotland]: [Galashiels].

**camoenaeformis** (if)—*Pararge aegeria egerides italica camoenaeformis* Verity, 1919—042:127.

***cantabricola** (ra)—*Erebia philomela cantabricola* Verity, 1927—064:174—Syntypes 6♂♂, 1♀ [Spain]: Asturias: [Puerto] Pajares: 1300 m: 6-8 VIII [19]24: Romei [leg]—Warren (1936): form of *Erebia euryale antevortes* Verity, 1927.

**carboncina** (if, ra)—*Erebia gorge carboncina* Verity, 1916—031:54—[Italy]: Mti. Sibillini: Fonte della Pescola: 20 VII 1911—Higgins (1976): *Erebia gorge carboncina* [nec Verity], subspecies.

**castanea** (if)—*Coenonympha tullia castanea* Verity, 1953—120:122.

**castaneaparvorientalis** (sf, if)—*Lasiommata maera parvorientalis castaneaparvorientalis* erity, 1938—108:11—Syntype ♀ [Beyrut?]; *castaneaparvoriantalis.*

**castaneopicta** (if)—*Pararge megera vividior castaneopicta* Verity, 1923—048: 25—[Spain, Italy]—Rank and original combination confused.

**celtibera** (ra, tf)—*Hipparchia briseis celtibera* Verity, 1927—064:175—Syntypes 5♂♂, 3♀♀ [Spain]: Aragon: [Prov. Teruel]: Albarracin: 1100 m: 3-20 VII 1924: Querci [leg.].

***centralasiae** (ra)—*Coenonympha pamphilus centralasiae* Verity, 1926—057: 205—Syntypes 5♂♂, 2♀♀ [U.S.S.R.]: Fergana: Alai.

***centralis** (ra)—*Coenonympha pamphilus centralis* Verity, 1926—057:204—Syntyps 4♂♂, 2♀♀ [France]: Vendee: Chemtonay: 8-29 V 1918.

***cephalidarwiniana** (ra)—*Coenonympha arcania cephalidarwiniana* Verity, 1953—120:101—Syntypes 2♂♂, 1♀ [France]: Beses-Alpes: Lac d'Allos: 1 VII [19]33; Alpes-Maritimes: Boreo: Satlage, Cascade: 27 VII [19]35, 19 VII [19]35; [all] Gazel [leg.].

***claradentata** (ra)—*Arethusana erythia claradentata* Verity, 1953—120:294—Syntypes 3♂ Espana: Nueva Castilla: Cuenca: Fernandez [leg.]; rest of type-series destroyed by museum pests.

***claramaritima** (ra)—*Nytha arethusa claramaritima* Verity, 1929—073:199—Holotype ♂, Paratype ♀ [France]: N.-O. de Nice: Bar-sur-Loup.

**claratropos** (if)—*Agapetes russiae atropos claratropos* Verity, 1953—120:59.

**clarephisius** (sr)—*Hyponephele lycaon ephisius clarephisius* Verity, 1953—120: 243—Syntypes 10♂♂, 7♀♀ [Italy: Torino]: Alpi Cozie: Val Susa: Oulx [= Ulzio]: 1100 m: 10 VII-7 VIII [19]25; Verity [leg.]; Alpi Cozie: Cesana: 1300 m: 1 VIII [19]25: Verity [leg.].

**conspicua** (ra)—*Nytha actaea ferula conspicua* Verity, 1927—058:173—Syntypes 10♂♂, 5♀♀ [N. Italy]: Vanzone: 11 VII-17 VIII 1924.

***conspicuella** (ra)—*Karanasa ferula conspicuella* Verity, 1935—094:63—Syntype 7♂♂, 3♀♀ [Switzerland]: Vaud: Bex, Sepey: 1-17 VIII 1932, 27 VII 1933: [Verity leg.].

**corinnaeformis** (if)—*Coenonympha pamphilus australis aestivus corinnaeformis* Verity, 1915—028:228—Italy: Toscana: Lago di Porta nella Versilia: 30 VIII 1914.

**corinnanorax** (sf)—*Coenonympha corinna corinna corinnanorax* Verity, 1953—120:108—Italy: Sardegna.

**crasseantelimbata** (if)—*Agapetes arge arge crasseantelimbata* Verity, 1953—120:51—Syntypes 1♂, 1♀ [Italy]: Lazio: Formia: 10 V [19]46.

**crassemaculosa** (if)—*Satyrus statilinus allionia crassemaculosa* Verity, 1917—034:189—Syntypes 4♀♀ [Italy]: Spezia: Isola del'Tino: 5 & 23 IX [19]05.

**crassolimbo** (if)—*Coenonympha arcania tenuelimbo crassolimbo* Verity, 1953—120:99—Syntype ♀ [Italy]: Firenze: Pian di Mugnone: 17 V [19]17, 19 V [19]45: Verity, Querci [leg.].

***crattiae** (ra)—*Erebia aethiops crattiae* Verity, 1923—049:135—Syntypes 1♂, 2♀♀ [Italy: Alpi Cozie: Torre Pellice]: Val d'Angrogna: 8-16 VIII [19]06—Warren treated *crattiae* as junior subjective synonym of *Erebia aethiops salaria* Fruhstorfer 1917.

**CRETUS** (nn)—*Satyrus briseis cretus* Verity, 1913—022:206—Replacement name for *Satyrus briseis major* Oberthür, 1876, which Verity erroneously considered secondary junior homonym of *Papilio hermionemajor* Esper, 1777, treated in combination *Satyrus hermione major* (Esper 1777); Esper's name was originally published hyphenated thus: *hermione-major.*

***degener** (ra)—*Hyponephele lycaon degener* Verity, 1927—058:123—Syntypes 4♀♀ [Switzerland]: Zermatt: 1600 m, 1800 m: 3-14 VIII 1911.

***depressivaga** (ra)—*Erebia aethiops depressivaga* Verity, 1935—094:56—Syntypes 6♂♂, 4♀♀ [Switzerland]: Vaud: Bex: 24 VII-15 VIII [19]32, 14-17 VIII [19]33: Verity [leg.].

**detersa** (if)—*Coenonympha pamphilus lyllus lyllides detersa* Verity, 1915—028:226—Italy: Rovescio.

**diffusa** (if)—*Agapetes psyche pherusa difusa* Verity, 1953—120:55—Syntype ♀ [Italy: Sicily]: Palermo: s. Martino: V.

**egestasioformis** (if)—*Pararge aegeria egerides italica egestasiformis* Verity, 1919—042:127—Holotype(?) destroyed by museum pests.

**elegantiaeformis** (if)—*Pararge aegeria egerides italica elegantiaeformis* Verity, 1919—042:127—Holotype(?) destroyed by museum pests.

***ellineata** (ra)—*Eumenis allionii ellineata* Verity, 1927—102:100—Syntypes 2♂♂ [Turkey]: Pontus, Amasia.

**emialbina** (if)—*Erebia aethiops emialbina* Verity, 1915—028:217—Holotype ♀ Germania; type: *emialbina.*

***emiaustralis** (ra)—*Coenonympha pamphilus emiaustralis* Verity, 1919—042:121—Syntypes 3♂♂ [Switzerland]: Geneve: Versoix: 22 V 1910, 21 V 1915.

***emihispulla** (ra)—*Epinephele jurtina emihispulla* Verity, 1919—042:123—Syntypes 60♂♂, 26♀♀ [Italy]: Isola d'Elba: Poggio: 400 m: 21 V-19 VII 1916; all remounted and relabelled—Thomson (1973): *Maniola jurtina emihispulla* [nec

Verity], subspecies.

**emilianus** (nomen nudum)—*Minois briseis emilianus* Verity, 1925 [nec Fruhstorfer]—055:115—Name attributed to H. Fruhstorfer, published without description, definition or indication.

***emilianus** (ra)—*Eumenis brisis emilianus* Verity, 1937—103:12—Holotype ♂ [Italy]: Modena: Cargedolo: 6 VIII [19]01: Costnatini [leg.].

**emilyllus** (ra, sf)—*Coenonympha pamphilus emilyllus* Verity, 1919—042:121—Syntypes 27♂♂, 21♀♀ [Italy]: Firenze: Pian di Mugnone: 6 VII-15 VIII 1916; all remounted and relabelled.

***emilyssa** (ra)—*Pararge megera emilyssa* Verity, 1919—042:126—Syntype ♂ Turquie [= Turkey]: [Bosporus]: 30; type: *emilyssa*—Larsen (1974): *Lasiommata megera emilyssa* [nec Verity], subspecies.

**erynisoculata** (sr)—*Erebia gorge erynis erynisoculata* Verity, 1953—120:169—Syntypes 4♂♂ [Italy: Alpi Retiche: Passo dello] Spluga: VII [19]08, VIII [19]10: Costantini [leg.]; Switzerland: Engadina: Val Gronda: Oberhalbstein: 4 VII 1908.

**essonsakaria** (sr)—*Agapetes galathea sakaria essonsakaria* Verity, 1953—120: 78—Syntypes 4♂♂, 1♀ [Italy: Alto Adige: Tirolo: Trento]: Vetriolo [Bagni]: VIII [19]08: [Verity leg.].

***etruriae** (ra)—*Erebia stygne etruriae* Verity, 1919—042:124—[Italy: Toscana]: Abetone.

**ETRUSCA** (ssp)—*Erebia neoridas etrusca* Verity, 1904—004:55—Syntypes 3♂♂, 1♀ [Italy: Toscana]: Alpi Apuane: M. Matana: VII [1]901, VIII [1]902, VIII [1]903: [Verity leg.]—Original rank 'var.' treated as subspecies by implication; also Warren (1936) recognized *etrusca* at subspecies-rank.

***etrusca** (ra)—*Pyronia tithonus etrusca* Verity, 1919—042:123—Syntypes 20♂♂, 14♀♀ [Italy]: Firenze: Fontebuona di Vaglia: [Monte Conca]: 400 m: 18 VII-9 VIII 1914: [Querci leg.]; all remounted and relabelled.

**euxina** (ra, sf)—*Coenonympha pamphilus euxina* Verity, 1926—057:207—Syntype ♂ [Turkey]: Asia Minor: Kastamuni [= Katamonu].

**exiliterpicta** (if)—*Agapetes russiae japygia exiliterpicta* Verity, 1953—120:60—Syntypes 2♂♂, 2♀♀ [Italy]: Lazio: Monte meta: Larocca: Fonte: 28 VII [19]40; Abruzzi: Monte Portella: 2100 m: 5 VIII [19]42.

**extensa** (if)—*Agapetes psyche pherusa extensa* Verity, 1953—120:54—Syntype ♂ [Italy: Sicily]: Palermo: S. Martino; *extensa*.

**exterfusca** (if)—*Coenonympha tullia exterfusca* Verity, 1953—120:122—Holotype ♂ [Germany]: Berlin; 'olotipo': *exterfusca*.

**exteriusocellata** (if)—*Melanargia galathea galinthias exteriusocellata* Verity, 1920—046:56—Holotype ♂ [Italy: Molise: Campobasco]: S. Pietro Avellana: 27 VII [19]19; type: *exteriuscocellata*.

**extralunulata** (if)—*Pararge maera vulgaris appennina extralunulata* Verity, 1920—046:57—Holotype(?) ♀ Italia centrale: Monti Aurenci: Valle del petrella: Casetta: 1000 m: 30 V 1911; type: *extralunulata*.

***fatuaeformis** (ra)—*Satyrus statilinus fatuaeformis* Verity, 1919—042:129—Syntypes 1♂, 1♀ As[ia] Minore: Fanasti.

***ferrea** (ra)—*Coenonympha pamphilus ferrea* Verity, 1926—057:202 Syntypes

13♂♂, 7♀♀ [Italy]: Lago Maggiore: Intra: Pian Quaggie: 950 m: 1-20 VI 1922; Lago Maggiore: Cannero: Passo di Colle: 1245 m: 28 VI-6 VII 1922: [all] Verity [leg.].

**ferulaeformis** (if)—*Nytha actaea ferulaeformis* Verity, 1927—058:174—Syntype ♂ [France: Marseilles: Septemes].

**fidiaeformis** (if)—*Satyrus statilinus fidiaeformis* Verity, 1919—042:128—Syntypes 2♂♂ [France: Alpes-Maritimes]: Grasse.

***filiplumemilyssa** (ra)—*Pararge megera filiplumemilyssa* Verity, 1953—120:31—Syntypes 6♂♂, 2♀♀ [Italy]: Costa Trieste: Venezia Giulia: Opicina: Carso: 18 VII [19]26, 25 VIII [19]26; [Yugoslavia]: Istria: Portorose [= Portoroz]: 3-8 IX [19]26.

***fiorii** (ra)—*Coenonympha tullia fiorii* Verity, 1953—120:123—Syntypes 2♂♂ , 2♀♀ [Italy: Alpi Carnice: Lago Inferiore]: Tarvisio: Fucina: [770 m]: 7 VII [1]951.

***florentia** (ra)—*Hyponephele lupinus florentia* Verity, 1937—106:45—Syntypes 11♂♂, 2♀♀ Italia centrale: Toscana: Firenze: Fiesole: Monte Fanna: 600-650 m: 15 VII 1917, 1 IX [19]13, 5 VIII [19]29; Firenze: Monte Senaria: 24 VII [1]903; [all] Querci, Verity [leg.].

***florentina** (ra)—*Melanargia galathea florentina* Verity, 1919—042:125—Syntypes 65♂♂, 50♀♀ Italia centr.: [Toscana]: Firenze: Pian di Mugnone: 200 m: 1 VI-6 VII 1915: Querci [leg.]; most of specimens remounted and relabelled.

**foeda** (ra, sf)—*Coenonympha pamphilus foeda* Verity, 1926—057:203—Syntypes 11♂♂, 6♀♀ [Spain]: Catalonia: Santa Fe: 1200 m: 3-31 VII [19]25; Catalonia: Seva: 700 m: 19 VII-2 VII [19]25; Catalonia: Montseny: 600 m: 17-18 IX [19]25; [all] Querci [leg.].

**fulvappennina** (nomen nudum)—*Pararge maera appennina fulvappennina* Verity, 1953—120:37—Name for seasonal form published without description, definition or indication.

**fulvolactea** (ra, sf, if)—*Coenonympha pamhilus fulvolactea* Verity, 1926—057: 205—Syntypes 4♂♂ Transkasp.: Kuschk—Rank confused but certainly infrasubspecific.

**fulvornata** (if)—*Brintesia circe fulvornata* Verity, 1953—120:285—Holotype ♂ [Italy]: Sardegna: Cagliari.

***fulvosatura** (ra)—*Coenonympha arcania fulvosatura* Verity, 1935—094:52—Syntypes 4♂♂, 3♀♀ [France: Gironde]: St. Come: 1920, 15 VII 1927, 24-29 VI 1929.

**fulvovittata** (if)—*Coenonympha dorus fulvovittata* Verity, 1953—120:105—Holotype ♂ [Italy]: Liguria: Bardineto: 1 VIII [1]910: Fiori [leg.]; 'olotipo': *fulvovittata.*

**fulvovittata** (if)—*Hyponephele lycaon lycosura fulvovittata* Verity, 1953—120: 240—Holotype ♂ [Italy: Alpi Marittime: Terme di] Valdieri: [1375 m]: 29 VII [19]11: [Verity leg.]; 'olotipo': *fulvovittata.*

**fuscelegantia** (if)—*Pararge aegeria camoena fuscelegantia* Verity, 1953—120: 18—Syntypes 3♂♂, 5♀♀ [France: Alpes-Maritimes]: St. L[aurent]-du-V[ar]: c.p.t.p.: 25 V [19]32; [Italy]: Torino: Venaria: T. Stura: 29 V 1936, 29 V 1932: Rocca, Rocci [leg.]; [Italy: Milano: Ticino]: Turbigo: 19-26 V [19]35: Rocci [leg.].

***gaillardi** (ra)—*Hyponephele lycaon gaillardi* Verity, 1929—072:186—France: Lozere: Concoule; Aigoual: Lercepede.

***gigas** (ra)—*Coenonympha pamphilus gigas* Verity, 1919—042:122—Syntype ♀ [Italy]: Sicilia: [illegible]: Ragusa [leg.]: 7; type: *gigas.*

***gigas** (ra)—*Pararge achine gigas* Verity, 1935—094:60—[Italy]: Torino: Venaria Park.

**gracilis** (if, sf)—*Coenonympha arcanius tenuelimbo gracilis* Verity, 1919—042: 123—Syntype(?) ♂ [Italy]: Spezia: Lerici: 19 VIII [19]13: Verity [leg.].

**grandescens** (nomen nudum)—*Pararge megera grandescens* Verity, 1923—048: 24—Name proposed for 'secondary race' published without description, definition or indication.

**grandescens** (if)—*Pararge megera vividior grandescens* Verity, 1953—120:24—Syntypes 1♂, 1♀ [N. Italy]: Luino: 4 IX [18]99; Alpi Pennine: Vanzone: 700 m: 17 VIII [19]28: Verity [leg.].

**herdoniaepar** (sr)—*Pararge maera orientalpina herdoniaepar* Verity, 1953—120:40—[Italy: Südtirol]: Terlan.

***hibera** (ra)—*Hipparchia semele hibera* Verity, 1923—051:156—Syntypes 5♂♂, 1♀ Espana: Nueva Castilla: Cuenca, Canizares: Fernandez [leg.].

***hyperleuca** (ra)—*Eumenis briseis hyperleuca* Verity, 1937—103:59—Syntypes 1♂, 1♀ [Turkey]: Asia Minor: Yozgat: pine woods: 5000 ft.: VII 1918: Capt. W. W. Phillips [leg.]: 1919-92; duplicate N.D.R.: [ex BM(NH)].

**infracanens** (if)—*Pararge megera praeaustralis infracanens* Verity, 1923—048: 28—Peninsular Italy.

***infracastanea** (ra)—*Eumenis allionii infracastanea* Verity, 1938—109:14—Syntypes 2♀♀ [Greece]: Macedonia: Salonica [= Thessaloniki]: 1000 ft.: 8 VIII 1936: Romei [leg.].

***infraclara** (ra)—*Erebia pandrose infraclara* Verity, 1953—120:132—Syntypes 12♂♂, 1♀ [N. Italy: Alpi Carniche]: Sappada: Val Milbach, Passo Dicola, Passo Sesis, Passo Sierra: 1600-2000 m: 4-8 VII [19]35, 10 VII [19]35, 20 VII-8 VIII [19]36: Rocca, Rocci [leg.].

**infradiffusa** (if)—*Erebia tyndarus majellana infradiffusa* Verity, 1953—120: 161—Holotype ♀ [Italy]: Abruzzi: [Gran Sasso]: Mte Portella: 2100 m: 13 VIII [19]42; 'olotipo': *infradiffusa.*

**infraestivalis** (sf)—*Coenonympha pamphilus emiaustralis infraestivalis* Verity, 1926—057:204—Switzerland: Martigny.

***infrafusca** (ra)—*Pyronia tithonus infrafusca* Verity, 1937—104:229—Syntypes 3♂♂ [N. Italy]: Torino: Rivoli; Bergamo: Sonbuono: [illegible]: 20 VII [19]29: [Verity leg.].

***infrafuscissima** (ra)—*Pyronia tithonus infrafuscissima* Verity, 1937—104:228—Syntypes 2♂♂, 2♀♀ [N. Italy]: Lago Maggiore: Ghiffa: 18 VIII 1932, Intra: 26 VII [19]33: [all] Verity [leg.].

***infragrisea** (ra)—*Pyronia tithonus etrusca infragrisea* Verity, 1937—104:232—C. Italy: Firenze (vic.) and other localities.

**infralbosparsa** (if)—*Erebia medusa infralbosparsa* Verity, 1953—120:180.

**infralbovittata** (if)—*Minois dryas infralbovittata* Verity, 1953—120:289—Holotype ♀, paratype ♂ Italia settentrionale: Alto Adige: [Bozen]: Atzwang: 30 VII 1920—Verity confused sexes on labels.

***inframilada** (ra)—*Karanasa ferula inframilada* Verity, 1935—094:63—Syntypes 11♂♂, 11♀♀ [Switzerland]: Valais: Martigny[-Ville]: 18-31 VII 1932, 10 & 18

VII 1933: Verity [leg.].

**infranigrans** (if)—*Pararge aegeria egerides italica infranigrans* Verity, 1920—046:57.

***infrapallens** (ra)—*Pararge megera infrapallens* Verity, 1922—048:211—Syntypes 5♂♂ Maroc: Meknes: [Middle Atlas Mts.]: Foum Kheneg: VII [1]920; Algeria: Mascara: VII; some specimens have incomplete or partially illegible data.

**infrarasa** (ra, sf)—*Coenonympha pamphilus centralis infrarasa* Verity, 1926—057:206—Syntypes 2♂♂, 2♀♀ [U.S.S.R.: C. Asia]: Saraw[shan] sept.: Raigorodsk: Juli.

***infrargentea** (ra)—*Erebia tyndarus infrargentea* Verity, 1919—042:125—Syntypes 19♂♂, 11♀♀ [Italy]: Marche: Monti Sibillini: [Bolognola]: 1200-2200 m: 26 VI-6 VIII 1913, 10 VIII 1918: [Querci leg.]; data on specimen labels agree only partly with data stated in original description.

**infratersa** (if)—*Pararge megra infratersa* Verity, 1923—048:27—Italy: Sicily.

**infrauniformis** (if)—*Minois dryas infrauniformis* Verity, 1953—120:289—Syntypes 1♂, 1♀ [N. Italy]: Alpi Pennine: Vanzone: 700 m: 20 VIII [19]28: Verity [leg.].

**insubridarwiniana** (if)—*Coenonympha arcania gardetta insubridarwiniana* Verity, 1927—060:70—Syntype ♀ [N. Italy]: Lago Maggiore: Cannero: Passo di Colle: 1245 m: 6 VII 1922: Verity [leg.]—Original combination and rank confused, in 1953 treated by Verity (120:102) as race.

***interjecta** (ra)—*Hipparchia briseis interjecta* Verity, 1919—042:129—Syntypes (?) 1♂, 1♀ [France]: Royan: M. Moul; Charente.

**intermedia** (if)—*Satyrus statilinus apennina intermedia* Verity, 1920—045:270—Syntypes 3♂♂, 1♀ [Italy: Toscana: Firenze]: Vallmbrosa: [900 m]: VIII 1905: Verity [leg.].

***itala** (ra)—*Satyrus circe itala* Verity, 1919—042:129.

**ITALICA** (ssp)—*Coenonympha typhon italica* Verity, 1915—028:222—Syntypes (?) 2♂♂ Italia centrale: Piceno: Monti Sibillini: 1700 m: 14-16 VI 1913; both specimens destroyed by museum pests, remnants of their damaged wings glued to a card apparently by Verity himself—Davenport (1941): *C. tullia italica*, subspecies.

***italica** (ra)—*Pararge aegeria italica* Verity, 1916—033:167—Syntypes 12♂♂, 4♀♀ [Italy]: Firenze: 28 III [19]13, 9 V [19]13, 5-11 IV [19]15: Verity, Querci [leg.]; some specimens remounted and relabelled.

**juldusica** (ra, sf)—*Coenonympha pamphilus centralasiae juldusica* Verity, 1926—057:206—syntypes 6♂♂, 3♀♀ [U.S.S.R.: C. Asia]: Juldus: Kuldscha.

***latealba** (ra)—*Pararge achine latealba* Verity, 1935—094:59—Syntypes 3♂♂ [France]: Auzay.

**latecana** (if)—*Coenonympha pamphilus semilyllus latecana* Verity, 1926—057:204—Syntypes ♀ [France]: Alpes-Maritimes: La Rognete: VII 1920; type: *latecana*.

**latefulva** (if)—*Coenonympha dorus latefulva* Verity, 1953—120:105—Holotype(?) ♀ [Italy]: Alpi Marittime: Triora: 27 VII [19]47: Prola [leg.].

***latenigrata** (ra)—*Coenonympha pamphilus latenigrata* Verity, 1919—042:122—[S. Europe: ?].

***latevittata** (ra)—*Satyrus alcyone latevittata* Verity, 1911—017:312—Syntypes 3♂♂, 1♀ [Italy: Toscana]: Ap[pennino] Lucchese: Pisarone: [Verity leg.]; data partly illegible.

**latevittata** (sf, if)—*Coenonympha pamphilus latevittata* Verity, 1916—033:172—[N. Africa: Algeria]; apparently described from a single specimen received from Le Cerf and now lost or destroyed.

***latiusalba** (ra)—*Eumenis briseis latiusalba* Verity, 1937—103:51—Syntypes 1♂, 2♀♀ [Turkey]: Asia Min[or] c.: Ak-Chehir: 1-10, 20-31 VII 1928: Coll. Wagner, Wien.

**lineolata** (if)—*Pararge aegeria vulgaris lineolata* Verity, 1953—120:13— [Italy]: Lazio: Atina: 500 m.

**londinii** (ra, sf)—*Coenonympha pamphilus londinii* Verity, 1926—057:205—Syntypes 3♂♂, 1♀ [England: Essex]: Osyth: Hartley Wood: VII 1870: Conquest [leg.].

**longocellata** (if)—*Hipparchia statilinus longocellata* Verity, 1953—120:329—Italy: Viareggio.

**luteafilipluma** (nomen nudum)—*Pararge megera lutefilipluma* Verity, 1923—048:28—Name for 'grade' in variation or transitional form published without description, definition or indication.

**luteavividior** (nomen nudum)—*Pararge megera luteavividior* Verity, 1923—048:28—Name for 'grade' in variation or transitional form published without description, definition or indication.

**luteavividissima** (nomen nudum)—*Pararge megera luteavividissima* Verity, 1923—048:28—Name for 'grade' in variation or transitional form published without description, definition or indication.

**lyllides** (sf)—*Coenonympha pamphilus lyllus lyllides* Verity, 1915—028:226—Syntype ♀ [Italy]: Sardegna: Lanusei: III [1]904.

**lylliformis** (sr, if)—*Coenonympha pamphilus lyllus lylliformis* Verity, 1953—120:115—Syntypes 3♂♂, 4♀♀ [France: Var]: Nimes: Tholozan [and other localities in the area, names illegible]: 27 VII-1 VIII 1926: Gaillard [leg.].

***macroleucocinia** (ra)—*Lasiommata maera macroleucocinia* Verity, 1935—094: 61—Syntypes 12♂♂, 7♀♀ [Switzerland]: Vaud: [Martigny]: Bex: St. Triphon: [on meadows]: 9-25 VII [19]32, 3 VI-11 VII [19]33: Verity [leg.].

**macromma** (if)—*Coenonympha arcania macromma* Turati & Verity, 1911—015:237—Syntypes 14♂♂, 4♀♀ [Italy: Alpi Marittime]: Valdieri: VIII [18]98, 25 VII, 20 VIII [19]09, 14-28 VII [19]11: Verity [leg.].

**macrommata** (sr)—*Erebia medusa generosa macrommata* Verity, 1953—120: 183—Italy: Bergamo.

**macronereus** (sr)—*Agapetes galathea nereus macronereus* Verity, 1957—116: 454—Syntypes 2♂♂, 6♀♀ [France]: Gard: Aignes-Montes: 24 VI [19]28, 23 VI-13 VII [19]35; [France: Bouches-du-Rhone]: Les Iseles: 29 VI [19]24: [all] Gaillard [leg.].

***macrophtalma** (ra)—*Coenonympha dorus macrophtalma* Verity, 1935—120: 106—Syntypes 5♂♂, 2♀♀ [France]: Nice: 8 VIII [1]901, 21 VII [19]39; [Italy]: Liguria: Bardineto: 1 VIII 1910, Alpi Marittime: Carmo Langan: 25 VII [19]47, Triora: 27 VII [19]47; Fiori, Prola, Verity [leg.].

**macrosciritis** (sr)—*Agapetes galathea sciritis macrosciritis* Verity, 1953—120:72—

Syntypes 9♂♂, 5♀♀ [Italy: Lazio]: Roma: Farensina: 100 m: 16 VI [1]901, 6 VI [1]913, 22 V-2 VIII 1939: Rocci, Rostagno, Romei [leg.].

**macrosiscia** (nomen nudum)—*Erebia ligea siscia macrosiscia* Verity, 1953—120:226—Name for subrace published without description, definition or indication.

***maesta** (ra)—*Coenonympha arcania maesta* Verity, 1927—060:40—Syntypes 4♂♂ [France: Pyrenees]: Gedre: VI [19]16: Rondou [leg.]—Name for 'transitional race'.

**magnavivida** (sr)—*Satyrus actaea actaea magnavivida* Verity, 1953—120:274—Syntypes 16♂♂, 5♀♀ [France]: Gallia mer.: St. Martin-Ves[ubie]: Coll. Höfer, Wien.

***magnobscura** (ra)—*Hyponephele lycaon magnobscura* Verity, 1929—072:186—Syntypes 12♂♂, 6♀♀ [Italy: Alto Adige: Bolzano]: Alpi Retiche: Bormio: 1300 m: 3-11 VIII [19]27: Verity [leg.].

**magnocellata** (if)—*Erebia neoridas magnocellata* Turati & Verity, 1911—015: 227—[Italy: Alpi Marittime]: Valdieri; holotype(?) destroyed by museum pests.

**magnocellata** (sr)—*Erebia neoridas neoridas magnocellata* Verity, 1953—120: 143—Syntypes 18♂♂, 1♀ [Iatly]; Alpi Maritime: Terme Valdieri: 3-16 VIII [19]38: Verity [leg.].

**magnocellata** (if)—*Pararge megera vividior magnocellata* Verity, 1953—120:25—Holotype ♀ [N. Italy]: Alpi Pennine: Vanzone: 700 m: 17 VII [19]28: Verity [leg.].

**magnorientalpina** (sr)—*Paparge maera orientalpina magnorientalpina* Verity, 1953—120:40—Syntypes 2♂♂, 4♀♀ [all] [N. Italy]: Tarvisio: 16 VI [18]67, 4 VII [19]45, 20 VII [1]951; Dolomity: Val Gardena: S. Ulrico: Ortisei: 1250 m: 20 VII 1923; Frassine: 1200 m: 12 VII [19]38; Alpi Carniche: Forni Avoltri: [900 m]: 7 VII [19]36; Zeller, Rocci [leg.].

***marenigrans** (ra)—*Maniola telmessia marenigrans* Verity, 1938—108:9—Syntypes 22♂♂, 7♀♀ [Turkey]: Asia Min[or] c.: Ak-Chehir: 30 V-28 VI [????]: Wagner [leg.]—Original description split between years 1937 and 1938, text published in 1937 inadequate to constitute a description; name spelled *marinigrans* in 1937 and *marenigrans* in 1938.

**mariformis** (if)—*Nytha actaea ferula orsiera mariformis* Verity, 1927—058:173—Syntypes 9♂♂, 21♀♀ [N. Italy: Alpi Marittime]: Valdieri: 31 VII-25 VIII [19]09, 28 VII [19]11: Verity [leg.].

**marinigrans** (ra)→**marenigrans** (ra)

**marmorea** (if)—*Satyrus statilinus allionia marmorea* Verity, 1917—034:189—Holotype ♂ [Italy]: Spezia: St. Bartolomeo: 18 VIII [19]13: [Verity leg.]; type: *marmorea*.

***maxima** (ra)—*Aphantopus hyperantus maxima* Verity, 1916—033:171—Syntypes 1♂, 3♀♀ [Italy]: Torino: Venaria: 10-13 VII 1911.

**mediocontracta** (if)—*Pararge maera mediocontracta* Verity, 1953—120:34.

***medioitalica** (ra)—*Melanargia japygia medioitalica* Verity, 1915—028:216—Syntypes 19♂♂ Italia centrale: Piceno: Monti Sibillini: Pian di Gra: 1300 m: 15 VII-6 VIII 1913: Querci [leg.]; rest of type-series apparently lost, including all specimens from Pizzo Tre Vescovi.

**melanojapygia** (if)—*Agapetes russiae japygia melanojapygia* Verity, 1953—120: 59—Syntypes 1♂, 1♀ [Italy]: Lazio: Monte Meta: Fonte Larocca: 1000 m: 14 VII

[19]40; Sicily: Palermo: Ragusa.

**meolansella** (sr, if)—*Erebia meolans meolans meolansella* Verity, 1953—120: 137—[Italy]: Liguria di Levante: Chiavari: Monte Penna.

***micromaritima** (ra)—*Satyrus statilinus micromaritima* Verity, 1919—042:128—Syntypes 22♂♂, 3♀♀ Italia centrale: Toscana: Lucca: Forte dei Marmi: 2 m: 24-31 VIII 1917, VIII [19]02: Verity [leg.]; most of specimens remounted and relabelled.

***micromeridionalis** (ra)—*Eumenis briseis micromeridionalis* Verity, 1937—103: 14—Syntypes 3♂♂, 5♀♀ [Italy]: Firenze: Monte Fanna: 1 IX [19]13, 5 VIII [19]29.

***micronosandrus** (ra)—*Nytha statilinus micronosandrus* Verity, 1927—058: 174—Syntypes 6♂♂ [Italy]: Alpi Cozie: Val Susa: Oulx [= Ulzio]: 1100 m: 11-16 VIII 1926: Verity [leg.].

***microprocida** (ra)—*Melanargia galathea microprocida* Verity, 1919—042:125—Syntypes 3♂♂, 3♀♀ [S. Italy]: Benevento: VII [19]18; rest of type-series probably lost.

***microsakaria** (ra)—*Melanargia galathea microsakaria* Verity, 1927—058:126—Syntypes 3♂♂ Italia settentrionale: Alto Adige: Mendola Pass: 23 VII [19]20, Klotenstein: 19 VII [19]20.

**microsciritis** (sr)—*Agapetes galathea sciritis microsciritis* Verity, 1953—120:72—Syntypes 10♂♂, 12♀♀ [Italy: Abruzzi]: Gran Sasso: 1300-1700 m: 11 VII-12 VIII 1939; Aquila: Monte Majella: 1600 m: 17 VII 1926; Monte Portelli: 2100 m: 5-8 VIII [19]42; Sirente: Monte Rotondo: 1400-1500 m: 23 VII-3 VIII [19]41: Romei [leg.].

**minusoculata** (if)—*Pararge achine minusoculata* Verity, 1953—120:19.

**minuta** (if)—*Erebia ligea minuta* Verity, 1953—120:222.

**minutior** (sr)—*Chazara briseis micromeridionalis minutior* Verity, 1953—120: 300—Syntypes 13♂♂, 11♀♀ [Italy]: Marche: Bolognola: 5-25 VIII 1937: Querci [leg.]; Abruzzi: Gran Sasso: 1300 m: 9 VII-16 VIII 1939: Romei [leg.].

***minutula** (ra)—*Eumenis statilinus minutula* Verity, 1938—108:13—Syntype 1♂ [Turkey]: Asia Min[or] c.: Ak-Chehir: 21-31 VII 1938: Coll. Wagner, Wien; rest of syntypes probably destroyed by museum pests or lost.

***miscens** (ra)—*Maniola jurtina miscens* Verity, 1953—120:268—Syntypes 1♂, 7♀♀ [France]: Alpes Maritimes: St. Barnabe: 19 VI [19]34: Gazel [leg.]; 11-17 VIII [19]37: Verity [leg.].

**monoantepupillata** (if)—*Satyrus statilinus allionia monoantepupillata* Verity, 1917—034:190—Italy: Elba.

**monocellata** (if)—*Hipparchia statilinus monocellata* Verity, 1953—120:328—Holotype ♂ [Italy: Genova]: Quezzi: 22 VIII [1]912; 'olotipo': *monocellata*.

**monostriata** (if)—*Satyrus statilinus allionia monostriata* Verity, 1916—034:190—Italy: Isola d'Elba.

***monticola** (ra)—*Melanargia galathea monticola* Verity, 1919—042:125—Syntypes 9♂♂, 7♀♀ [Italy: Toscana]: Firenzuola: 25 VI-15 VIII 1916.

**murina** (if)—*Coenonympha pamphilus australis murina* Verity, 1915—028:228—Italy: Firenze.

**nana** (if)—*Agapetes arge arge nana* Verity, 1953—120:50—[Italy]: Lazio: Formia: VI.

**neoridasoides** (if)—*Erebia montanus neoridasoides* Verity, 1953—120:145—

Italy: Alpi Marittime: Terme di Valdieri.

***nereine** (ra)—*Satyrus galathea nereine* Verity, 1935—094:58—Syntype(?) ♂ [Switzerland]: Barisal: [1600 m]: 20 VII [19]33: Verity [leg.].

**nigerrima** (if)—*Satyrus neomiris nigerrima* Verity, 1917—034:188—Italy: Isola d'Elba.

***nigrionereus** (ra)—*Satyrus galathea nigrionereus* Verity, 1935—094:58—Syntypes 30♂♂, 22♀♀ [Switzerland]: Valais: [Martigny]: Bex: 30 VI-9 VIII [19]32, 15 VI [19]33: Verity [leg.].

**nigrogenava** (sr)—*Hipparchia aelia genava nigrogenava* Verity, 1953—120:326—Syntypes 3♂♂, 4♀♀ [Italy: Modena]: Appeninno Modenese: Le Pozze: 22 VIII [19]09: Costantini [leg.]; Monte Penna: 16-19 VII [19]33, 25 VII [19]35: Rocci [leg.].

**nitidissima** (ra, sf)—*Coenonympha pamphilus nitidissima* Verity, 1926—057: 199—Syntypes 6♂♂, 1♀ Syrien [= Lebanon]: Beyruth.

***norica** (ra)—*Satyrus statilinus norica* Verity, 1919—042:128—Syntypes 1♂, 1♀ Austria infer[ior]: VIII [????].

**nuragiformis** (if)—*Epinephele jurtina janira nuragiformis* Verity, 1916—033: 169—Holotype ♀ [Italy: Lago Maggiore]: Intra: 5 VII [1]906; type: *nuragiformis.*

**ocellaris** (if)—*Coenonympha arcania macromma ocellaris* Turati & Verity, 1911—015:238—Syntype ♂ [Italy: Alpi Marittime]: Valdieri: 16 VII 1911: [Verity leg.]; type: *ocellaris.*

***ocellatior** (ra)—*Pararge megera ocellatior* Verity, 1923—048:24—[France]: Gers: Lectoure.

**OPPOSITA** (ssp)—*Coenonympha arcanius apposita* Verity, 1915—028:223—Syntypes 8♂♂, 5♀♀ Italia merid.: Calabria: Aspromonte: 1200 m: 14-23 VII 1914: Querci [leg.]—Not considered worthy of recognition at subspecies-rank by Davenport (1941).

**orba** (if)—*Erebia pandrose orba* Verity, 1953—120:129.

***orientalpina** (ra)—*Satyrus maera orientalpina* Verity, 1927—058:156—Syntypes 15♂♂ 11♀♀ [N. Italy]: Alpi Carniche: Sappada: 1300 m: 8 VII-6 VIII [19]26: Verity [leg.].

**orientalpium** (ra)—*Nytha actaea ferula orientalpium* Verity, 1927—058:173—Syntypes 2♂♂, 1♀ [N. Italy]: [Süd]tirol: Val Venosta: Tschan, Schnalstal: Astfäller [leg.].

***padi** (ra)—*Nytha statilinus padi* Verity, 1927—058:175—Syntypes 1♂, 1♀ [Italy]: Brescia: Capriolo.

***paeninsulitaliae** (ra)—*Hipparchia semele paeninsulitaliae* Verity, 1924—051: 24—Syntypes 4♂♂, 1♀ Italia centrale: [Firenze]: Fiesole: Monte Fanna: 650 m: 15 VII 1917, 2 VIII 1917, 12 VII 1918: Querci [leg.].

**paeninsulitalica** (sf)—*Pararge megera praeaustralis paeninsulitalica* Verity, 1923—048:24—Italy: Firenze: Pian di Mugnone.

***pallidalgirica** (ra)—*Hipparchia semele pallidalgirica* Verity, 1923—051:155—Syntypes 4♂♂, 1♀ Algeria: Lambese: VI 1907: Dayrem [leg.].

***pallidedepulverata** (ra)—*Pararge megera pallidedepulverata* Verity 1923—048:28—N. Africa, S. Spain—Name for 'transitional race'.

**pallidephisius** (sr)—*Hyponephele lycaon ephisius pallidephisius* Verity, 1953—

120:243—Syntypes 1♂, 1♀ [Italy]: Modena: Bastia: 30 VII [19]12; Ligorzano: 19 VII [19]12; [both] Costantini [leg.].

***pannonica** (ra)—*Satyrus hiera pannonica* Verity, 1927—058:157—Syntypes 2♂♂, 2♀♀ Ungheria [= Hungary]: Kormeczbanja: 31 V [1]911, 8 VII [1]918; some specimens with incomplete data.

***panormitana** (ra)—*Melanargia galathea panormitana* Verity, 1919—042:125—Syntypes 4♂♂, 1♀ [Italy]: Isola di Sicilia: Palermo: San Martino: Monreale: 800 m: 9 VI 1918: Querci [leg.]; some specimens with incomplete data.

***paracleo** (ra)—*Erebia tyndarus paracleo* Verity, 1927—058:124—Italy: Alpi Cozie: Ulzio.

***paratransiens** (ra)—*Pyronia tithonus paratransiens* Verity, 1937—104:225—Syntypes 3♂♂, 4♀♀ [France]: Marseille: Septemes, Nans: 24 VII 1932, 6 VIII 1935, 8 VIII [19]31, 9 VIII 1936.

**parumgenerosa** (sr)—*Erebia medusa generosa parumgenerosa* Verity, 1953—120:184—Syntypes 2♂♂, 1♀ [Italy]: Lago di Maggiore: Cannero: Passo di Cole: 1245m: 2 VII 1922: Verity [leg.].

***parvalpestris** (ra)—*Pararge hiera parvalpestris* Verity, 1929—072:188—Syntypes 2♀♀ [N. Italy]: Alpi Carniche: Sappada: 1300 m: 13-15 VII [19]26: Verity [leg.].

**parvavivida** (sr)—*Satyrus actaea actaea parvavivida* Verity, 1953—120:274—Syntypes 1♂, 1♀ [France]: Alpi Marittime: Carmo Langan: 25 VII 1947: Prola [leg.].

**parvinsubrica** (ra, sf)—*Coenonympha arcania parvinsubrica* Verity, 1927—060:39—Syntypes 8♂♂, 2♀♀ [N. Italy]: Alpi Carniche: S. Stefano [di Cadore]: 900-1100 m: 16-17 VII [19]26; Sappada: Cima: 1400 m: 22 VII [19]26; [all] Verity [leg.].

***parvisi** (ra)—*Erebia aethiops parvisi* Verity, 1915—028:217—Syntypes 2♂♂ [N. Italy: Udine]: Arta: [500 m]: VII 1910.

***parvorientalis** (ra)—*Lasiommata maera parvorientalis* Verity, 1938—108:11—Holotype ♂ Siria [= Lebanon]: Beyrouth; tipo: *parvorientalis.*

**parvorientalpina** (sr)—*Satyrus maera orientalpina parvorientalpina* Verity, 1927—058:156—Syntype ♀ Italia settenrionale: Alto Adige: Mendola Pass: 21 VII [19]20: [Verity leg.]; type: *parvorientalpina*—Originally designated 'secondary race' and, probably, described from single specimen.

***paulumaegeria** (ra)—*Pararge aegeria paulumaegeria* Verity, 1957—116:433—Syntypes 2♂♂, 1♀ [France: Maine-et-Loire]: Saumur: 20 VI 1892; Bretagne: Marbidan: Vaunes: Joannis [leg.]; Sarthe: Avoise: 16 IV 1914: Coll. Abot.

**pauper** (if)—*Epinephele jurtina janira pauper* Verity, 1916—033:169—Holotype ♀ [Switzerland]: Vallese: [Martigny]: Wulfschlegel; type: *pauper.*

***pedemontii** (ra)—*Melanargia galathea pedemontii* Verity, 1927—058:125—Syntypes 6♂♂, 4♀♀ [N. Italy]: Torino: Venaria: 10 VII 1911, 23-29 VI [19]23; Valdieri: VIII [18]98, 15-20 VIII 1909: Verity [leg.].

**pedenereine** (sr)—*Agapetes galathea nereus pedenereine* Verity, 1953—120:79—Syntype ♂ [N. Italy: Aosta]: Val Tornenza: VII [1]917.

**pedenereus** (sr)—*Agapetes galathea nereus pedenereus* Verity, 1953—120:79—Syntypes 1♂, 2♀♀ [Italy: Piemonte: Aosta]: Courmay[eur]: 20 VII [19]20, 15-21 VII [19]24, Rocci [leg.].

**permagnocellata** (if)—*Epinephele lycaon permagnocellata* Turati & Verity, 1911—015:236—Syntype ♀ [N. Italy: Alpi Marittime: Terme di] Valdieri: 25 VIII [19]11: [Verity leg.]; type: *permagnocellata.*

***persiscana** (ra)—*Eumenis allionii persiscana* Verity, 1937—102:100—Lectotype ♂, paralectotypes 1♂, 4♀♀, designated by Kudrna (1977) Iran: Elbursgebirege: Keredj: [1500 m]: 25 VIII 1936: Brandt leg.—Misspelled and treated as subspecies by Kudrna (1977): *Hipparchia fatua persicana*, potential (conditional) subjective junior synonym of *Satyrus fatua klapperichi* Gross & Ebert, 1976.

**philedarwiniana** (ra)—*Coenonympha arcania gardetta philedarwiniana* Verity, 1927—060:70—Syntypes 8♂♂, 4♀♀ [N. Italy]: Lago Maggiore: Cannero: Passo di Colle: 1245 m: 28 VI-6 VII 1922: Verity [leg.].

**porrecta** (if)—*Pararge megera porrecta* Verity, 1919—042:126.

**postaurinensis** (sf)—*Pararge maera taurinensis postaurinensiss* Verity, 1953—120:41—N. Italy: Bergamo: Sombreno; Lago Maggiore: Intra: Bee; Chiavari: Monte Penna; Modena: Monte Gibbio.

**postaustralis** (sf, ra)—*Coenonympha pamphilus australis postaustralis* Verity, 1926—058:176—Italy: Alpi Cozie: Ulzio, Cesana, Clavieres.

**postaustralis** (sf, ra)—*Coenonympha pamphilus australis postaustralis* Verity, 1926—057:202—N. Italy: Alpi Cozie: Ulzio; Südtirol: Klobenstein: 1300 m, Meran.

**postbarcionis** (sf)—*Coenonympha pamphilus barcionis postbarcionis* Verity, 1926—057:203—Syntypes 16♂♂, 2♀♀ [Spain]: Catalonia: Llinas: 200 m: 3 VII-8 IX [19]25; Vilamajor: 300 m: 5-10 IX [19]25; [all] Querci [leg.].

**postcentralasiae** (sf)—*Coenonympha pamphilus centralasiae postcentralasiae* Verity, 1926—057:205—Syntypes 5♂♂, 1♀ [U.S.S.R.: C. Asia]: Fergana: Alai.

**postcentralis** (sf)—*Coenonympha pamphilus centralis postcentralis* Verity, 1926—07:204—Syntypes 3♂♂, 2♀♀ [France]: Eure: Pont-de-l'Arche: 1882, 1886; some specimens with incomplete data.

**postemiaustralis** (ra, sf)—*Coenonympha pamphilus postemiaustralis* Verity, 1926—057:204—Syntypes 5♂♂, 2♀♀ Schweiz: Neuchatel: Dombresson: VIII 1918, 8, 10, 17 IX [????]: Bolle [leg.].

**posteuxina** (sf)—*Coenonympha pamphilus euxina posteuxina* Verity, 1926—057:207—Syntypes 4♂♂ [Turkey]: Asia Minor: Yozgat: pine woods: 5000 ft.: VI-IX 1918: Capt. Phillips: 1919:92; [ex BM(NH)].

**postferrea** (sf)—*Coenonympha pamphilus ferrea postferrea* Verity, 1926—057:202—Syntypes 5♂♂, 2♀♀ [N. Italy]: Vanzone: [700 m]: 12 VII-15 VIII [19]24: [Verity lg.].

**postgalvagnii** (sf)—*Coenonympha pamphilus galvagnii postgalvagnii* Verity, 1953—120:119—Syntypes 20♂♂, 7♀♀ [Yugoslavia]: Portorosa [= Portoroz]: 1-16 IX 1926: Verity [leg.].

**postherdonia** (nomen nudum)—*Satyrus maera herdonia postherdonia* Verity, 1927—058:155—Name for seasonal form published without description, definition or indication.

**postherdoniaepar** (nomen nudum)—*Pararge maera orientalpina herdoniepar postherdoniaepar* Verity, 1953—120:40—Name for seasonal form published without description, definition or indication.

**posticecompleta** (if)—*Agapetes arge arge posticecompleta* Verity, 1953—120: 51—Holotype(?) ♀ [Italy]: Lazio: Formia: 10 V [19]46.

**postleucocinia** (sf)—*Satyrus maera leucocinia posleucocinia* Verity, 1927—058:155.

**postlondinii** (sf)—*Coenonympha pamphilus londinii postlondinii* Verity, 1926—057:205—Syntypes 8♂♂, 1♀ [England: London]: Middlesex: nr. Stamford Hill: 19 VIII 1887; Hornsey: 29 VIII 1875; Kent: [illegible]: 27-29 VIII 1876; [all] Conquest [leg.].

**postmacroleucocinia** (sf)—*Pararge maera leucocinia postmacroleucocinia* Verity, 1953—120:38—Italy: Genova: Savignone.

**postorientalpina** (sf)—*Satyrus maera orientalpina postorientalpina* Verity, 1927—058:156.

**postprotohiera** (sf)—*Pararge maera protohiera postprotohiera* Verity, 1953—120:41.

**postparvorientalis** (sf)—*Lasiommata maera parvorientalis postparvorientalis* Verity, 1938—108:11.

**postsilymbria** (sf)—*Satyrus maera silymbria postsilymbria* Verity, 1927—058: 156—Syntypes 5♂♂, 6♀♀ [Italy: Trieste]: Opicina: Carso: 25 VIII [19]26; [Yugoslavia]: Istria: Portorosa [= Portoroz]: 10 IX [19]26; [all] Verity [leg.].

**postsuperlata** (nomen nudum)—*Satyrus maera superlata postsuperlata* Verity, 1927—058:156—Name for seasonal form published without description, definition of indication.

**praeappennina** (sf)—*Pararge maeraappennina praeappennina* Verity, 1953—120:37—Syntypes 10♂♂, 10♀♀ [Italy: Toscana]: Appennino Pistoiese: Abetone: 1400 m: 11-20 VII [19]29: Verity [leg.].

***praehispulla** (ra)—*Epinephele jurtina praehispulla* Verity, 1921—042:210—Syntypes 44♂♂, 40♀♀ Italy: Firenze: Pian di Mugnone: 200 m: 29 V-21 VII 1915, 6 VI 1919: Querci [leg.]; all specimens remounted and relabelled.

**praeaustralis** (sf)—*Pararge megera praeaustralis* Verity, 1922—048:214—Syntypes 24♂♂, 5♀♀ Italia centrale: Toscana: Firenze: Pian di Mugnone: 200 m: 30 III-18 V 1917: Querci [leg.]; all specimens but 2♂♂ remounted and relabelled.

***presolanae** (ra)—*Erebia pronoe presolanae* Verity, 1953—120:153—[N. Italy]: Alpi Orobie: Lago d'Isneo: Pizzo della Presolana.

**privata** (if)—*Erebia epiphron cydamus privata* Turati & Verity, 1911—015:214—N. Italy: Alpi Marittime: Valdieri; described from a single specimen subsequently destroyed by museum pests.

***protohiera** (ra)—*Pararge maera protohiera* Verity, 1953—120:41—Name for race published without description, definition or indication.

**pseudodarwiniana** (nomen nudum)—*Coenonympha arcania darwiniana pseudodarwiniana* Verity, 1953—120:93—Name for race(?) published without description, definition or indication; original combination confused and rank intended uncertain.

**pulchrappennina** (sr)—*Erebia medusa hyperappennina pulchrappennina* Verity, 1953—120:183—Syntypes 4♂♂, 1♀ [Italy]: Modena: Le Radici: [1500 m]: 17 IV [19]12: Costantini [leg.]; Toscana: Appennino Pistoiese: Abetone: 1400 m: 7-19 VII [19]29: Verity [leg.].

***pulchravariegata** (ra)—*Nytha arethusa pulchravariegata* Verity, 1929—073: 199—Syntypes 1♀, 7♂♂ [S. France: Nimes]: Coll de Tir: 1 VIII [19]26, 31 VII [19]27; La Valborme: 8 VIII [19]26; Mas Bormiere: 7 VIII [19]27; [all] Gaillard [leg.].

***pyraenaica** (ra)—*Melanargia galathea pyraenaica* Verity, 1919—042:125—Syntypes 9♂♂, 1♀ [France]: H[autes]-P[yrenees]: Gedre: VII 1915, 8 VII 1916: Rondou [leg.]—Manley & Allcard (1970): *Melanargia galathea pyrenaica* [nec Verity], subspecies.

***pyrenaeorum** (ra)—*Hipparchia briseis pyrenaeorum* Verity, 1927—064:175—Syntypes 2♂♂ [France]: Pyr[enees]-Or[ientales]: Ambollos: 20 VII 1914—Manley & Allcard (1970): *Chazara briseis pyrenaeorum* [nec Verity], subspecies.

**quadripunctata** (if)—*Hipparchia neomiris quadripunctata* Verity, 1953—120: 315—Italy: Isola d'Elba.

**quaterocellata** (if)—*Erebia gorge quaterocellata* Verity, 1953—120:167.

***quercii** (ra)—*Hyponephele lycaon quercii* Verity, 1929—072:186—Syntypes 5♂♂, 12♀♀ Portugal: Serra da Estrela: 800-1000 m: 23 VII-27 VIII 1927: Querci [leg.].

**quinquiensocellata** (if)—*Erebia gorge erynis quinquiensocellata* Verity, 1953—120:167—Syntype ♂ [N. Italy]: Alpi Retiche: Passo dello Spluga: VIII [19]10: Costantini [leg.].

***remota** (ra)—*Hipparchia aelia remota* Verity, 1953—120:325—Syntypes 14♂♂, 3♀♀ Italy: Aspromonte: Piani di Carmelia: 1200 m: 12-27 VII 1914: Zucci [leg.]; all remounted and relabelled.

**ROSTAGNOI** (nn)—*Satyrus statilinus rostagnoi* Verity, 1919—042:128—Replacement name for *Satyrus statilinus maritima* Rostagno, 1911 said to be primary junior homonym of *Satyrus briseis maritima* Oberthür, 1909.

**rubrodiluta** (if)—*Erebia neoridas sibyllina rubrodiluta* Verity, 1953—120:143.

**SARDOA** (ssp)—*Pararge aegeria sardoa* Verity, 1909—012:114—Syntypes 1♂, 2♀♀ [Italy]: Sardegna: Cagliari—Name proposed for 'var.' and considered of subspecies-rank.

***scota** (ra)—*Satyrus semele scota* Verity, 1911—017:313—Syntypes 2♂♂, 2♀♀ Scizia [= Scotland]: Costa [illegible]: VIII [19]08.

***scota** (ra)—*Coenonympha pamphilus scota* Verity, 1911—016:271—Syntypes 3♂♂, 1♀ Scozia [= Scotland]: Costa sett.: VIII [19]08—Davenport (1941): *Coenonympha pamphilus scota* [nec Verity], subspecies.

**secunda** (sf)—*Coenonympha arcania tergestina parvinsubrica secunda* Verity, 1953—120:100—Syntypes 2♂♂, 1♀ [Italy: Torino]: Casal[borgone]: VIII [19]14.

***semibieli** (ra)—*Coenonympha dorus semibieli* Verity, 1929—072:185—Syntypes 26♂♂, 28♀♀ Portugal: Serra da Estrela: 800-1000 m: 13 VII-1 IX 1927: Querci [leg.]—Manley & Allcard (1970): *Coenonympha dorus semibieli* [nec Verity], subspecies.

***serena** (ra)—*Melanargia galathea serena* Verity, 1913—022:205—Syntypes 5♂♂, 3♀♀ England, Inghilterra: Abbots Ripton, Sussex: Abbot's Wood: 3 VII 1907; some specimens with incomplete data.

***sibyllina** (ra)—*Erebia neoridas sibyllina* Verity, 1915—028:236—Syntypes 30♂♂, 6♀♀ [Italy: Piceno]: Monti Sibillini: Bolognola: Piano Astore: 1100-1400 m: 14 VIII-6 IX 1913: [Querci leg.]—Warren (1936): *Erebia neoridas sibyllina* [nec Verity], subspecies.

**siculella** (sf)—*Coenonympha pamphilus sicula siculella* Verity, 1953—120:116—Syntypes 3♂♂ [Italy: Sicily]: Trabia: [50 m]: X.

**subalba** (if)—*Epinephele ida subalba* Verity, 1904—004:56—Holotype ♂ [Italy]: Toscana: [Viareggio]: Camaire: VIII 1902; Verity [leg.]; type: *subalba.*

**subalbida** (if)—*Epinephele tithonus subalbida* Verity, 1904—004:56—[Italy: Toscana]: Mt. Matanna.

***subcassioides** (ra)—*Erebia tyndarus subcassioides* Verity, 1927—058:124—Syntypes 15♂♂, 6♀♀ [Italy: Torino]: Alpi Cozie: Sestrieres: 2035 m: 8 VIII 1925: Verity [leg.]—Warren (1936): *Erebia tyndarus subcassioides* [nec Verity], subspecies.

***subcretus** (ra)—*Hipparchia briseis subcretus* Verity, 1927—064:175—Syntypes 3♂♂, 5♀♀ [Spain]: Andalucia: Sierra Nevada: Granada: 1200-1600 m: 15-27 VI 1925: Querci [leg.].

***superlata** (ra)—*Satyrus maera superlata* Verity, 1927—058:156—Syntypes 5♂♂, 6♀♀ [N. Italy]: Lago Maggiore: Cannere: Passo di Colle: 1245 m: 2-8 VII 1922; Mottarone: 8 VII [19]22; [all] Verity [leg.].

***taurinorum** (ra)—*Erebia aethiops taurinorum* Verity, 1911—017:312—Syntypes 4♂♂ [N. Italy]: Torino: Colli di Torino, Rivoli.

**telmessiaeformis** (nomen nudum)—*Epinephele jurtina telmessiaeformis* Verity, 1919—042:123—Name for race(?) published without description, definition or indication.

***tenebrogigas** (ra)—*Melanargia galathea tenebrogigas* Verity, 1938—109:13—Syntypes 1♂, 6♀♀ [Greece]: Macedonia: Olympus: 3500 ft.: 23 VI-17 VII 1936: Romei[leg.]—Name for somation or race.

***tenebronana** (ra)—*Melanargia galathea tenebronana* Verity, 1938—109:13—Syntypes(?) 4♂♂, 2♀♀ [Greece]: Macedonia: Naussa: Olympus: 2000-2500 ft.: 5-15 VII 1935: Romei [leg.]; status of all syntypes uncertain—Original rank uncertain, probably somation or race.

**TENEULIMBO** (ssp)—*Coenonympha arcanius teneulimbo* Verity, 1915—028:223—Syntypes 7♂♂, 1♀ [Italy: Piceno]: Monti Sibillini: [1700 m]: VI 1913: Querci [leg.]; [C. Italy]: La Traversa: 1000 m: 15 VII [19]13: [illegible]: [Verity leg.]—Not considered worthy of recognition at subspecies-rank by Davenport (1941).

***tergestina** (ra)—*Coenonympha arcania tergestina* Verity, 1927—060:40—Syntypes 5♂♂, 1♀ [Italy]: Costa Trieste: Venezia Giulia: Carso: Opicina: 1 VII [1]923, 26 VI [1]926, 10 VI [1]926, 18 VII 1926.

**terocellata** (if)—*Erebia gorge terocellata* Verity, 1953—120:167.

***tetrica** (ra)—*Erebia pirene tetrica* Verity, 1923—049:136—C. Italy: Monti Sibillini—Warren (1936): *Erebia meolans tetrica* [nec Verity], subspecies.

**tigeliclara** (if)—*Pararge megera tigeliclara* Verity, 1923—048:28—Syntype ♂ [Italy]: Sardegna.

**tigeliiformis** (if)—*Pararge megaera alticola tigeliiformis* Verity, 1911—016:269—Syntypes 5♂♂ [Italy: Toscana]: App[ennino] Pis[toiese]: [illegible]: 20 VIII-1 IX [19]11: [Verity leg.].

**tigellina** (sf)—*Pararge megera tigelius tigellina* Verity, 1922—048:213—Syntypes 5♂♂, 3♀♀ [Italy]: Sardegna: Lanusei, Ogliastro; some specimens with incomplete data, poorly legible.

**tigellyssa** (sf)—*Pararge megera australis tigellyssa* Verity, 1923—048:27—Syntype 3♂♂, 1♀ [Italy: Sicily]: Ficuzza: VIII [19]20.

**tithoniformis** (if)—*Epinephele jurtina janira tithoniformis* Verity, 1916—033:169—Holotype ♀ [Italy]: Sardegna: Ogliastro: 20 VII [19]04; type: *tithoniformis.*

**tornusdisjuncta** (if)—*Agapetes galathea galinthias tornusdisjuncta* Verity, 1953—120:66—Holotype(?) ♂ [Italy]: Lazio: Formia: 22 VI [19]38: Querci [leg.].

**torrida** (if, sf, ra)—*Coenonympha pamphilus torrida* Verity, 1911—016:271—[Italy]: Sardegna: Palao.

**totebrunnea** (if)—*Satyrus statilinus allionia totebrunnea* Verity, 1917—034:189—Italy: Isola d'Elba.

**toteflavivittata** (if)—*Satyrus neomiris toteflavovittata* Verity, 1917—034:188—Italy: Isola d'Elba.

**totefulvovittata** (if)—*Satyrus neomiris totefulvovittata* Verity, 1917—034:188—Italy: Isola d'Elba.

**totemaxima** (sr)—*Aphantopus hyperantus maxima totemaxima* Verity, 1953—120:237—Syntypes 6♂♂, 1♀ [Italy: Milano]: Turbigo: 15 VI [19]30, 22 VI [19]30, 27 VII [19]30: Rocci [leg.].

**totenigra** (sr)—*Erebia euryale ocellaris totenigra* Verity, 1953—120:217—Syntype 7♂♂ [N. Italy]: Dol[omoti] occ.: Val di Gares: Pian delle Giare: 1338 m: 5 VII 1937: Rocca [leg.].

**totenigrocellata** (if)—*Pararge megera totenigrocellata* Verity, 1953—120:25—Holotype ♀ [Greece]: Macedonia: Olympus: 14 VI 1935: Romei [leg.]; 'olotipo': *totenigrocellata.*

***transiens** (ra)—*Pyronia tithonus transiens* Verity, 1919—042:123—Syntypes 20♂♂, 7♀♀ [Italy]: Firenze: Pian di Mugnone: 200 m: 11 VII-9 VIII 1916: Querci [leg.]; all specimens remounted and relabelled—Original rank uncertain: transitional form or transitional race.

**triantepupillata** (if)—*Satyrus statilinus allionia triantepupillata* Verity, 1917—034:189—Italy: Isola d'Elba.

**triocellata** (if)—*Satyrus statilinus allionia triocellata* Verity, 1917—034:190—Holotype ♂ Italy: Elba: Bagnia: 5 VIII 1908; type: *triocellata.*

**tusca** (ra)—*Erebia tyndarus cassioides tusca* Verity, 1915—027:148—Syntypes 2♂♂, 5♀♀ [Italy: Modena]: Cimone: 27 VIII [19]12; [Toscana]: Teso: [above Cutigliana]: VIII 1900; Appennino Pistoiese: Abetone: [illegible].

**uniformis** (if)—*Pararge aegeria vulgaris uniformis* Verity, 1953—120:13—[Italy: Firenze]: Pian di Mugnone.

***valderiensis** (ra)—*Erebia goante valderiensis* Verity, 1919—042:124—Syntype ♂ [Italy: Alpi Marittime]: Valdieri: Vallasco: [1435 m]: 27 VII 1911; type: *valderiensis.*

***variegata** (ra)—*Satyrus arethusa variegata* Verity, 1929—017:313—Syntypes 5♂♂, 3♀♀ [France]: Lardy pres Paris: 27 VIII [????]; Eure: Pont-de-l'Arche: Alizay: 1916; same specimens with incomplete data.

**vernafusca** (if)—*Pararge aegeria vulgaris vernafusca* Verity, 1953—120:17—Italy: Firenze.

**vividior** (nomen nudum)—*Pararge megera vividior* Verity, 1923—048:23—Name for transitional form ('grade') published without description, definition or indication.

***vividior** (ra)—*Pararge megera vividior* Verity, 1953—120:30—Iberian Peninsula, S. France, N. Italy—Manley & Allcard (1970): *Lasiommata megera vividior* [nec Verity], subspecies.

**vividissima** (sf)—*Pararge megera vividissima* Verity 1923—048:25—S. Spain, N. Africa—Manley & Allcard (1970): *Lasiommata megera vividissima* [nec Verity], subspecies.

***vulgaris** (ra)—*Pararge maera vulgaris* Verity 1913—023:186—Syntypes 1♂, 4♀♀ [Italy: Toscana]: Firenze, Colline di Firenze: Verity [leg.].

**VULGOARETHUSA** (nn)—*Arethusana erythia vulgoarethusa* Verity 1953—120:293—Replacement name for *Papilio arethusa* Denis & Schiffermuller, 1775 which Verity erroneously believed to be unavailable.

***warreni** (ra)—*Erebia flavofasciata warreni* Verity 1923—049:136—[Switzerland]: Engadin: Tschierva Glacier.

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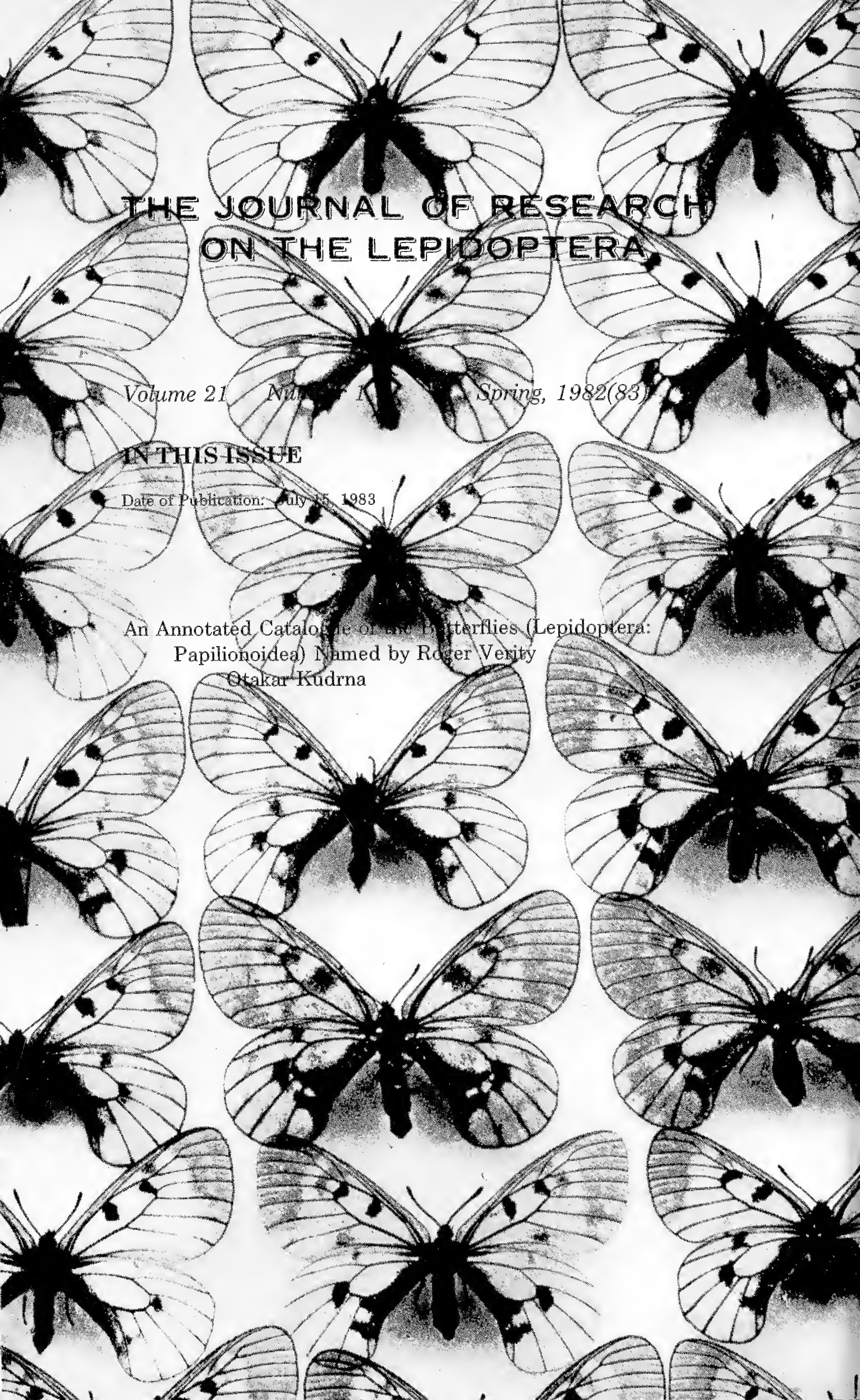

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Otakar Kudrna

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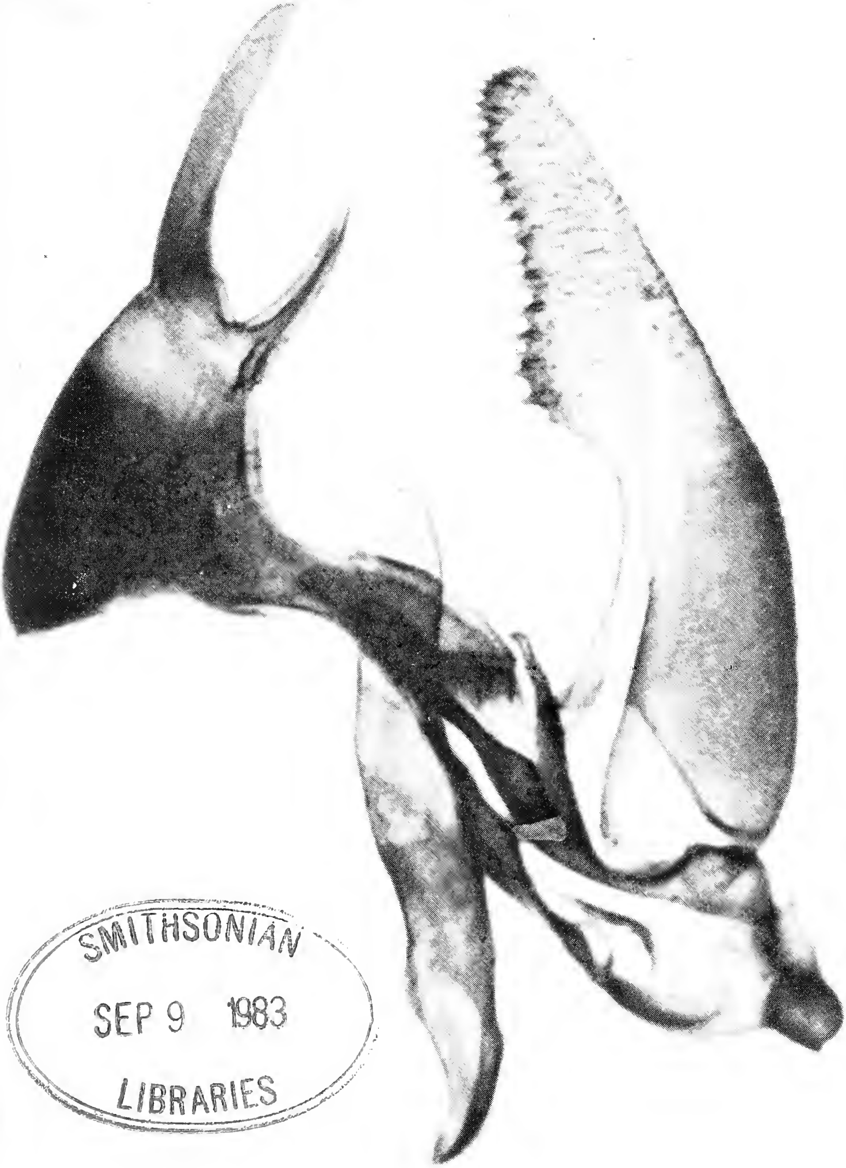

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# A Review of the *Erebia dabanensis* Complex (Lepidoptera: Satyridae), with Descriptions of Two New Species

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and

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**Abstract.** Considerable confusion exists in the literature associated with *Erebia youngi* (Holland, 1900) and *Erebia dabanensis* (Erschoff, 1861) in North America. This paper differentiates the five principal species previously grouped under these taxa and under *Erebia kozhantshikovi* (Sheljuzhko, 1925). Two new species are described: *Erebia lafontainei,* found on low shrub tundra throughout northern Alaska and adjacent Canada, and *Erebia phellea,* found on scree slopes throughout northern Alaska, northwest Canada, and in eastern Siberia.

## Introduction

Recent examination of various "*E. youngi*" phenotypes collected in North America has revealed that three closely related but distinct species occur in this group. Our study of Palearctic specimens of *E. kozhantshikovi* and *E. dabanensis* shows that, although *E. dabanensis* is *E. youngi*'s closest phenotypic neighbor, and *E. kozhantshikovi* is *E. lafontainei*'s closest phenotypic neighbor, significant differences can be found between these two sets of sister species and neither are conspecific.

Early authors (Warren, 1969; dos Passos, 1972) suggested that *E. dabanensis* did occur in North America. Dos Passos (1972) claimed the *E. youngi rileyi* (dos Passos, 1947) holotype to be *E. dabanensis*; however, our examination of the *E. youngi youngi* lectotype and the *E. youngi rileyi* and *E. youngi herscheli* (Leussler, 1935) holotypes has shown that these specimens are all conspecific, although the allotype and paratypes of *E. youngi rileyi* include both of our new species.

We now have long series of *E. youngi, E. lafontainei,* and *E. phellea* from many localities in Alaska and northwest Canada, as well as long series of Palearctic *E. dabanensis, E. kozhantshikovi,* and *E. phellea.* We are able at this time to compare lengthy series of all Palearctic and Nearctic species

---

[1] Standard Deviation.

within the *E. dabanensis* complex for the first time, and advance the work initiated by dos Passos and Warren. In order to clarify the confusion previously found in this complex, we describe two new taxa and give detailed diagnoses of the species and subspecies within this complex as follows.

## Key to Species

1a. VHW with distinct mesial and marginal bands; DFW fulvous ocelli with distinct black pupils, usually increasing in size from front to back; VFW ocelli fulvous to ruddy, never yellow; VHW hairs red to orange............................................................2

1b. VHW with obscure mesial and marginal bands (bands often more pronounced in populations from Denali Park, Alaska (formerly McKinley National Park), and the Bolshoi Annachag Range, Magadanskaya Oblast'); DFW fulvous ocelli with minute black pupils or pupils absent; however, when present, usually decreasing in size from front to back; VFW ocelli fulvous to yellow and very small; VHW hairs white to light brown; nudum of antenna with equal amounts of dark brown above and below a fine median ochre line (see Fig. 39); fringe of female checkered with dark brown at tips of veins; male genitalia with distal vertical processes of aedeagus sheath usually flat or slightly concave, valva narrowed at tip with many fine teeth across costa of ridge, this spined ridge averages 67.2% (range 62-72%) of costa of valva (see Figs. 50-55 & 58)................................**phellea**

2a. Nudum of antenna dark brown above median ochre line, ochre to dark brown below this median line (see Figs. 39, 41); ground color of male VHW postmedian-submarginal band dark brown with scattering of white scales which produces a hoary appearance; VHW mesial and marginal bands dark blackish brown to ruddy brown; fringe of female checkered with darker brown at tips of veins; male genitalia with distal vertical processes of aedeagus sheath usually flat or slightly concave, costa of valva rises abruptly (often at about 90°) to spined ridge............................................................3

2b. Nudum of antenna light ochre above and below a median dark brown patch (see Fig. 40); ground color of male VHW postmedian-submarginal band gray-brown, with a smooth, neat appearance, never hoary; VHW mesial and marginal bands medium brown to reddish-brown, never dark brown or blackish; male genitalia with distal vertical processes of aedeagus sheath usually greatly concave, costa of valva rises gradually to spined ridge............................4

3a. At present, known only from the Palearctic; pupils within DFW fulvous ocelli usually circular or oval; normally four large DHW ocelli with black pupils;male genitalia with valva elongated at tip and many coarse spines scattered across costa of ridge, this spined ridge averages 55.8% (range 47-67% of costa of valva (see Figs. 47, 58) ........................................................ **dabanensis**

3b. At present, known only from North America; pupils within DFW fulvous ocelli usually elliptical or oval; zero to five DHW fulvous ocelli with black pupils, (*E. youngi rileyi* with fewer HW ocelli than eastern races); male genitalia with tip of valva not elongated and many coarse or fine teeth scattered across ridge, this spined ridge averages 43.0% (range 36-47%) of costa of valva (see Figs. 46, 58).......... **youngi**

4a. At present, known only from the Palearctic; DFW normally has five submarginal fulvous ocelli with black pupils; VHW postmedian-submarginal band appears brown to gray-brown, with heavy scattering of light gray scales within cell $M_2$; VHW mesial and marginal bands appear medium brown to ruddy brown; four to five large DHW fulvous ocelli contain black pupils; fringe of female dark brown, rarely checkered with slightly darker brown at tips of veins; male genitalia with spined ridge normally not elevated above costa of valva to any great degree (see Figs. 49b-49d), and many very fine spines scattered across costa of ridge which averages 50.1% (range 44-56%) of costa of valva (see Figs. 49, 57, 58) ....................... **kozhantshikovi**

4b. At present, known only from North America; DFW normally has four submarginal fulvous ocelli with black pupils; VHW postmedian-submarginal band appears pinkish due to heavy scattering of pearlescent pink scales over a ground color of gray-brown; VHW mesial and marginal bands reddish-brown to maroon; zero to three small DHW ocelli with minute brown pupils or pupils absent; fringe of female never checkered with dark brown at tips of veins; male genitalia has spined ridge elevated well above costa of valva, many coarse spines scattered across costa of ridge, and costa of spined ridge usually slightly concave, this spined ridge averages 54.3% (range 50-59%) of costa of valva (see Figs. 48, 58) ....... **lafontainei**

## **Erebia dabanensis** Erschoff, 1871

### Diagnosis

Forewing length of male 21.1 ± 1.05[1] mm, range 19.1-23.0 mm (N = 20), and forewing length of female 21.4 ± 0.85 mm, range 20.0-23.0 mm (N = 12) (note: all above specimens from Bolshoi Annachag Range, Magadanskaya Oblast', U.S.S.R.).

*Erebia dabanensis* (Figs. 13-16, 34a, 34b) is characterized externally by the dorsal fulvous ocelli, containing black pupils which are more circular than those of *E. youngi* on the forewing and more numerous on the hindwing; by the ventral forewing submarginal fulvous ocelli, which are often coalesced into a broad fulvous band similar to that of *E. youngi*, while those of *E. kozhantshikovi* are never more than narrow fulvous halos which surround the black pupils; by the male's ventral hindwing, which is

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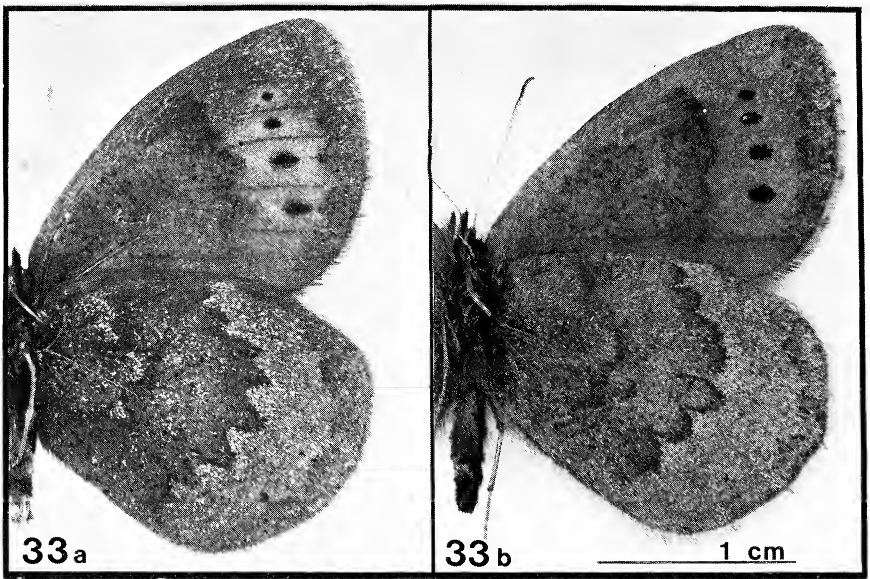
[1] Standard Deviation.



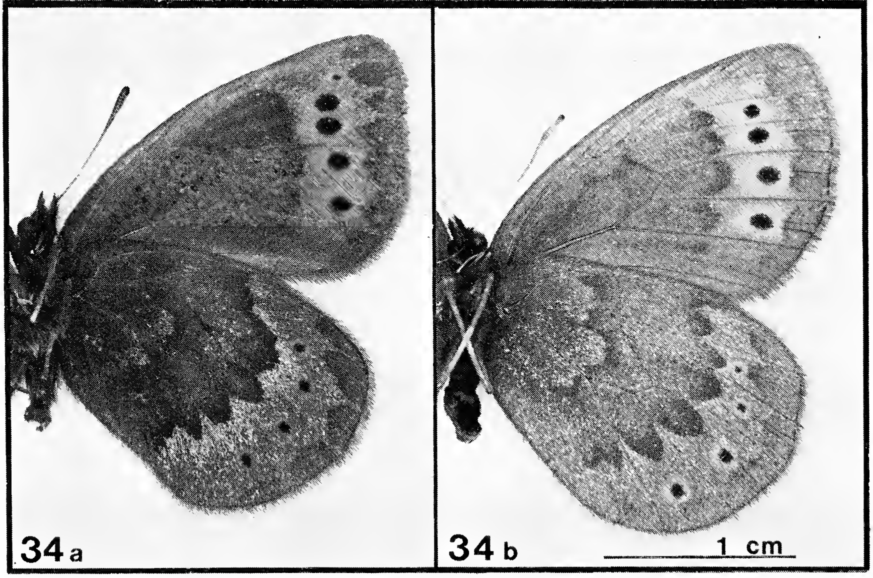
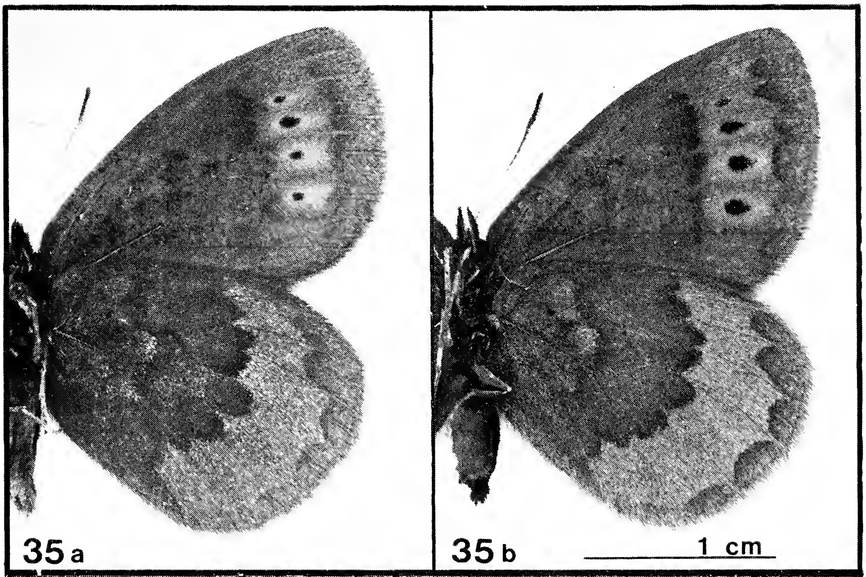


Fig. 33. *E. youngi*: (a) male ventral surface; (b) female ventral surface, both from Windy Pass, Ogilvie Mts., Yukon, 16 VI 1981, J. Troubridge, Leg.

Fig. 34. *E. dabanensis*: (a) male ventral surface; (b) female ventral surface, both from the Aborigen Station, Magadanskaya Oblast', 30 VI-24 VII 1980, K. Philip & A. Jones, Leg.



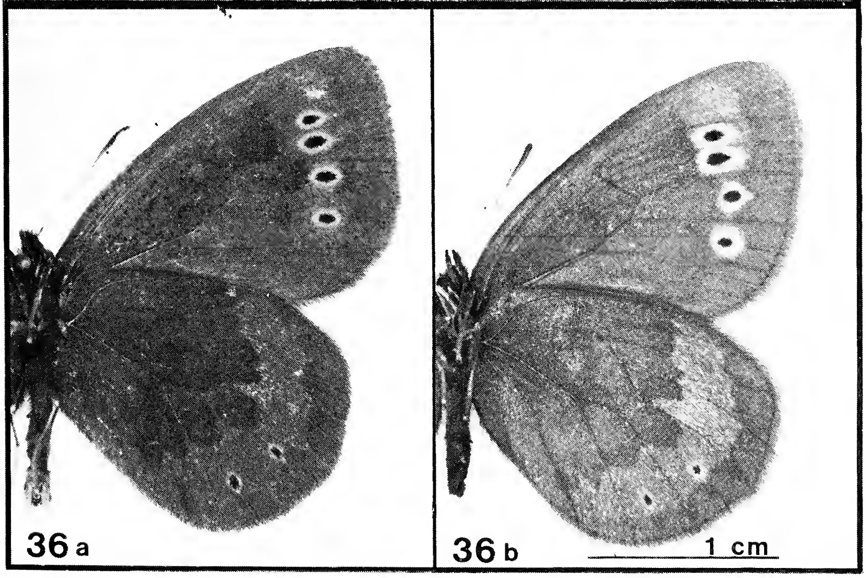
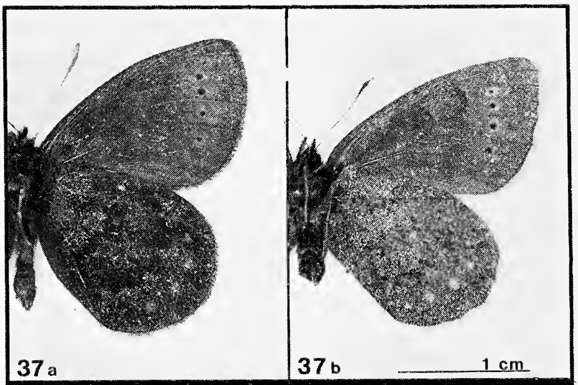


Fig. 35. *E. lafontainei*: (a) male ventral surface; (b) female ventral surface, both paratypes from Mt. Decoeli, St. Elias Mts., Yukon, 27 VI 1982, J. Troubridge & L. Lang, Leg.

Fig. 36. *E. kozhantshikovi*: (a) male ventral surface; (b) female ventral surface, both from the Aborigen Station, Magadanskaya Oblast', 28 VI 1978 (male) and 4 VII 1980 (female), K. W. Philip, Leg.



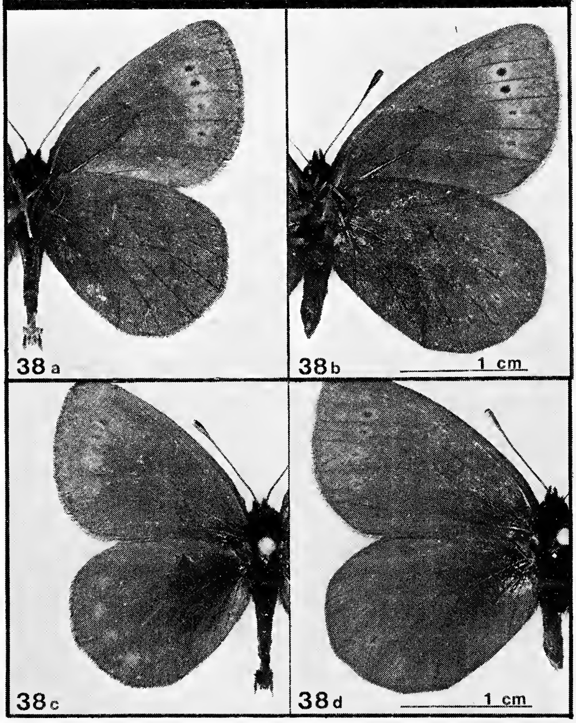


Fig. 37. *E. phellea*: (a) male ventral surface, mi 42, Council Rd., Seward Peninsula, Alaska, 29 VI 1971, D. G. Roseneau, Leg., (b) female ventral surface, Harris Dome, Seward Peninsula, Alaska, 2 VII 1971, K. W. Philip, Leg., both paratypes.

Fig. 38. *E. phellea*: (a) male ventral surface, (b) female ventral surface, (c) male dorsal surface, (d) female dorsal surface, all from the Aborigen Station, Magadanskaya Oblast', 29 VI-2 VII 1980, K. W. Philip & A. C. Jones, Leg.

grizzled with white scales in the postmedian and postbasal areas as in that of *E. youngi* (white scales absent in those of *E. lafontainei, E. youngi,* and most *E. phellea* from the Bolshoi Annachag Range); by the dark brown ventral hindwing color which overpowers the effect of the scattering of red scales as in *E. youngi* (*E. lafontainei* and *E. kozhantshikovi* appear reddish or maroon to light brown); by the distinct mesial and marginal ventral hindwing bands (obscure in most Nearctic *E. phellea* and many of the *E. phellea* from the Magadanskaya Oblast'); by the medial side of the antenna club, which is dark brown on the upper half and light ochre on the lower half similar to antennae of eastern races of *E. youngi* (Fig. 41) but very different from antennae of *E. lafontainei, E. kozhantshikovi,* and *E. phellea* (Figs. 39, 40). The female is further characterized by the light brown fringe checkered with darker brown at the tips of the veins, similar to those of *E. phellea, E. youngi,* and a very few *E. kozhantshikovi* (checkering absent in *E. lafontainei*). Internally *E. dabanensis* is characterized by the male valva which is narrowed at the tip and has a raised, spined ridge which occupies 55.8 ± 5.6%, range 47-67% (N = 20) of the entire length of the costa (see Figs. 47, 58). The spined ridge usually drops back to the neck of the costa at an angle of about 90° to the costa as in that of *E. youngi*, although the tip of the valva is much longer, narrower, and more pointed than that of *E. youngi*, in which the spined ridge occupies only 36-47% of the costa length. The spines on the ridge of the valva of *E. dabanensis* do not venture below the costa on the outside edge as far as those of *E. phellea* and are much coarser and fewer in number than those of *E. phellea.*

## Distribution and Habitat

*Erebia dabanensis* ranges from the East Sayan Mountains to the Magadanskaya Oblast', northeastern Siberia. The type locality is the Khamar-Daban Range, just south of Lake Baikal (Buryatskaya, ASSR). Warren (1936) reports one record from the Polar Urals (Schuihya River) and one from the Anadyr Mountains, (now Chukotskii Range) on the Chukhotsk Peninsula—but he had not seen specimens and suspected that these records might refer to *E. kozhantshikovi*. K. Philip found this insect common in both taiga (open larch bog) and alpine tundra at the Aborigen Station, Bolshoi Annachag Range, upper Kolyma River, Magadanskaya Oblast', U.S.S.R., and the Alaska Lepidoptera Survey (ALS) collection has additional material (from Soviet volunteer collectors) from the Detrin River, Stokovoye, and Vetrenyy. All of these sites lie within the Okhotsk-Kolyma Uplands, north of Magadan.

Kurentzov (1970) reports that in the northeast of the Magadanskaya Oblast' *E. dabanensis* is replaced by *E. tundra* (Staudinger, 1887)—but Kurentzov appears to have been somewhat confused about both of these species as well as *E. kozhantshikovi* (see below under *E. tundra* for details) and until the material in Kurentzov's collection is checked, one cannot rely on his determinations in this group.

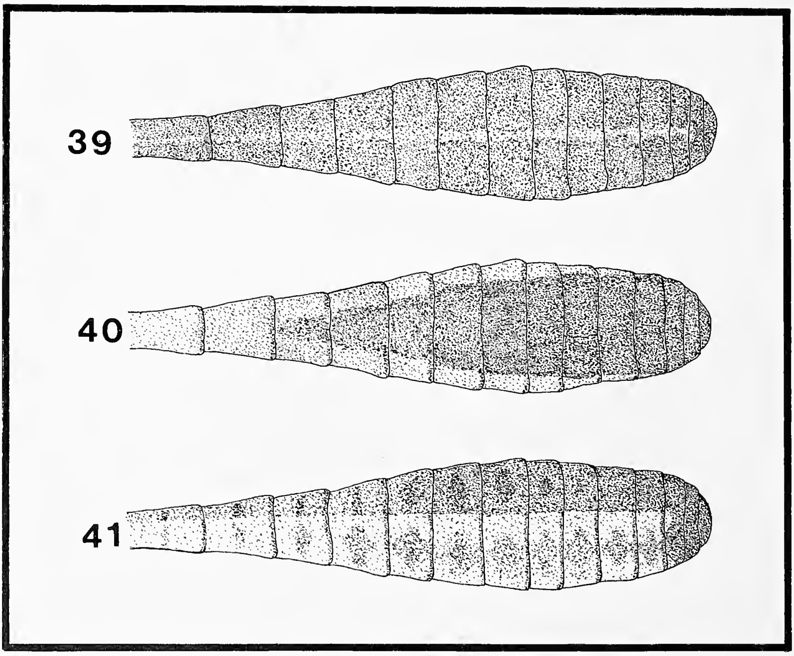
The flight period is late June to late July.

## **Erebia youngi youngi** Holland, 1900

### Diagnosis

Forewing length of male 20.2 ± 1.2 mm, range 18.0-23.5 mm (n = 20), and forewing length of female 20.1 ± 1.1 mm, range 17.5-22.0 mm (N = 20) (all specimens from the Ogilvie Mts., Yukon Territory, Canada).

*Erebia youngi* (Figs. 1-4, 33a, 33b) is characterized externally by the bright fulvous submarginal ocelli of the dorsal forewing which contain large elliptical or oval black pupils, the anterior two usually smaller than the posterior two as in those of *E. lafontainei* and *E. dabanensis*; by the ventral forewing, which has a wide submarginal fulvous patch rather than a series of fulvous submarginal ocelli; by the submarginal fulvous ocelli of the dorsal hindwing which average larger in size and number than those of *E. lafontainei* and *E. phellea* (but smaller and fewer in number than those



Figs. 39-41. Medial side of antenna club of: (39) *E. phellea* and most specimens of *E. youngi rileyi*; (40) *E. lafontainei* and *E. kozhantshikovi*; (41) *E. dabanensis, E. youngi youngi,* and *E. youngi herscheli.* Although the pattern on the medial side of the antenna club may be faded to obscurity in a very few specimens, when present, this pattern will always approach one of the above figures.

of *E. dabanensis* and *E. kozhantshikovi*) and contain black pupils, not dark brown as in those of *E. lafontainei*; by the male's ventral hindwing, which has a blackish brown overall appearance as in that of *E. dabanensis* and *E. phellea*, although the mesial and marginal bands are usually much more pronounced than those of *E. phellea*; by the scattering of white scales in the postbasal and postmedian areas of the ventral hindwing which produces a hoary appearance as in that of *E. dabanensis*; and by the medial side of the antenna club, which is dark brown on the upper half and light ochre on the lower half (Fig. 41) as in that of *E. dabanensis*. Females and some males are further characterized by the fringe, which is checkered with darker brown at the tips of the veins as in females of *E. phellea, E. dabanensis,* and (rarely) *E. kozhantshikovi* (checkering absent in *E. lafontainei*).

Internally, *E. youngi* is characterized by the male valva which is not extended at the tip (extended in *E. phellea, E. dabanensis, E. kozhantshikovi,* and *E. lafontainei*). For this reason, the spined ridge on the valva of *E. youngi* occupies the least percentage of the total length of the costa of the entire complex at 43.0 ± 2.0%, with a range of 36-47% (N = 20). The shoulder of the spined ridge drops back to the neck of the valva at about 90° to the costa as in that of *E. dabanensis*, not at a gentle angle as in those of *E. phellea, E. lafontainei*, and *E. kozhantshikovi*. The spines may be fine or coarse (Figs. 46a-46d) and well separated or touching, depending on the individual.

## Distribution and Habitat

*Erebia youngi* is found in dry tundra meadow and tundra fellfield habitats from the Richardson Mts., British Mts., Ogilvie Mts., and St. Elias Mts. of Canada's Yukon, west through the Brooks Range of Alaska, at least as far as Walker Lake in the Endicott Mts. (Fig. 42). The type locality is the mountains between Fortymile and Mission Creeks, Alaska (near the Alaska/Yukon border, roughly west of Dawson, Yukon).

The flight period is late June to late July.

## Remarks

Dos Passos (1972) dissected two male syntypes of *E. youngi* and assigned one as the *E. youngi* lectotype and determined the other to be *E. dabanensis*. Our examination of these specimens shows that the *E. youngi* lectotype fits our concept of *E. youngi* (as it must), but the male syntype which do Passos determined to be *E. dabanensis* is *E. lafontainei*. A third *E. youngi* syntype in the Carnegie Museum, a female, is a specimen of *E. youngi*.

## **Erebia youngi herscheli** Leussler, 1935

## Diagnosis

Forewing length of male 20.0 ± 1.1 mm, range 18.5-21.5 mm (N = 20) (all specimens from Herschel Island, Yukon Territory).

*Erebia youngi herscheli* (Figs. 5-8) is a distinct subspecies, characterized externally by the dull ochre-brown forewing ocelli which average smaller and darker than those of *E. youngi youngi*; by the very dull, obscure ventral hindwing which is chocolate-brown rather than blackish brown as in males of *E. youngi youngi*; and by the reduced amount of red around the black ocelli on the ventral forewing as in that of *E. youngi rileyi*. Internally, the male genitalia are identical to that of *E. youngi youngi*.

## Distribution

*Erebia youngi herscheli* appears to be a coastal race of *E. youngi* in Yukon. Specimens we have examined from Herschel Island, Yukon and Kay Point on the nearby mainland are the only populations which we have studied that would belong to this taxon. Six worn specimens in the American Museum of Natural History, nominally labelled Aklavik, 11 & 24 VII 31 (Owen Bryant) were placed as *E. youngi herscheli* by dos Passos (1947). *Erebia youngi* does not occur at Aklavik, a forested area in the Mackenzie Delta, although it is not uncommon in the Richardson Mts., less than 50 km west of Aklavik. The actual location for Bryant's 11 VII 31 specimens is Base Camp, Husky River, 40 km SW of Aklavik, and his 24 VII 31 specimens were collected at Black Mountain, 50 km SW of Aklavik. Although these specimens tend to approach *E. youngi herscheli*, they are in very poor condition and little can be said about their subspecific rank in certainty. Specimens we have examined in longer and fresher series collected north of, south of, and opposite Aklavik in the Richardson Mts. do not approach *E. youngi herscheli* and are all *E. youngi youngi*. We have deleted Bryant's "Aklavik" specimens from the distribution of *E. youngi herscheli* (Fig. 42) and place them as *E. youngi youngi*, although further collecting in the Black Mountains area may prove otherwise. We see no evidence of a cline between *E. youngi youngi* and *E. youngi herscheli* in the Richardson Mts. or British Mts. and regard *E. youngi herscheli* as a valid subspecies.

## Remarks

Leussler (1935) described *E. herscheli* as a distinct species from a series of three males collected from Herschel Island (O. Bryant). We have examined the holotype as well as a lengthy series (43 specimens) from Herschel Island and agree with dos Passos (1947) and Warren (1969) in that this race is conspecific with *E. youngi*.

After examining the holotype and two paratypes, dos Passos (1947) concluded that *E. youngi herscheli* usually has two rows of spines on the comb of the valva while *E. youngi youngi* has three, and that the spines are most numerous on the clasp of *E. youngi herscheli*, being closer together than on *E. youngi youngi*. Our examination of lengthy series of both races indicates that the number of teeth, their arrangement on the valva, and their fineness is extremely variable within any population and cannot be used in subspecific determination.

There is no difference in size between *E. youngi youngi* (FW length 20.2 ± 1.2 mm) and *E. youngi herscheli* (FW length 20.0 ± 1.1 mm) as suggested in the original description of *E. herscheli* (Leussler, 1935).

### **Erebia youngi rileyi** dos Passos, 1947

#### Diagnosis

Forewing length of male 21.5 ± 1.1 mm, range 19.5-24.0 mm (N = 20) (specimens from Denali National Park, Alaska).

*Erebia youngi rileyi* (Figs. 9-12) is distinguished from *E. youngi youngi* by the fulvous ocelli of the dorsal forewing which are usually smaller, duller, and contain smaller pupils than those of *E. youngi youngi*; by the fulvous ocelli of the ventral forewing, which are less often coalesced to form a broad submarginal band than those of *E. youngi youngi*; by the absence or reduced number of ocelli on the dorsal hindwing; by the ventral hindwing, on which the mesial and marginal bands are much more distinct, more heavily scalloped, and usually redder than those of *E. youngi youngi*; and by the antenna club, in which the nudum is usually equally dark above and below a light ochre median line as in that of *E. phellea* (Fig. 39). The male valva (Figs. 46b-46c) is similar to that of *E. youngi youngi*. The range of variation found in valva shape and spine coarseness (Figs. 46a-46d) is found in all populations of *E. youngi* that we have studied.

#### Distribution

*E. youngi rileyi* ranges from the type locality (Denali National Park) through the De Long Mountains and Cape Thompson areas of Alaska to the Seward Peninsula (Fig. 42). Specimens from extreme western Alaska differ from *E. youngi youngi* in the same characters as do specimens from Denali National Park; however, these differences are more extreme in specimens from the De Long Mountains and the Seward Peninsula and we do not hesitate to place them under this taxon. It is possible that a cline could exist between *E. youngi youngi* and *E. youngi rileyi* in the western Brooks Range, although we have not seen specimens that would suggest this.

#### Remarks

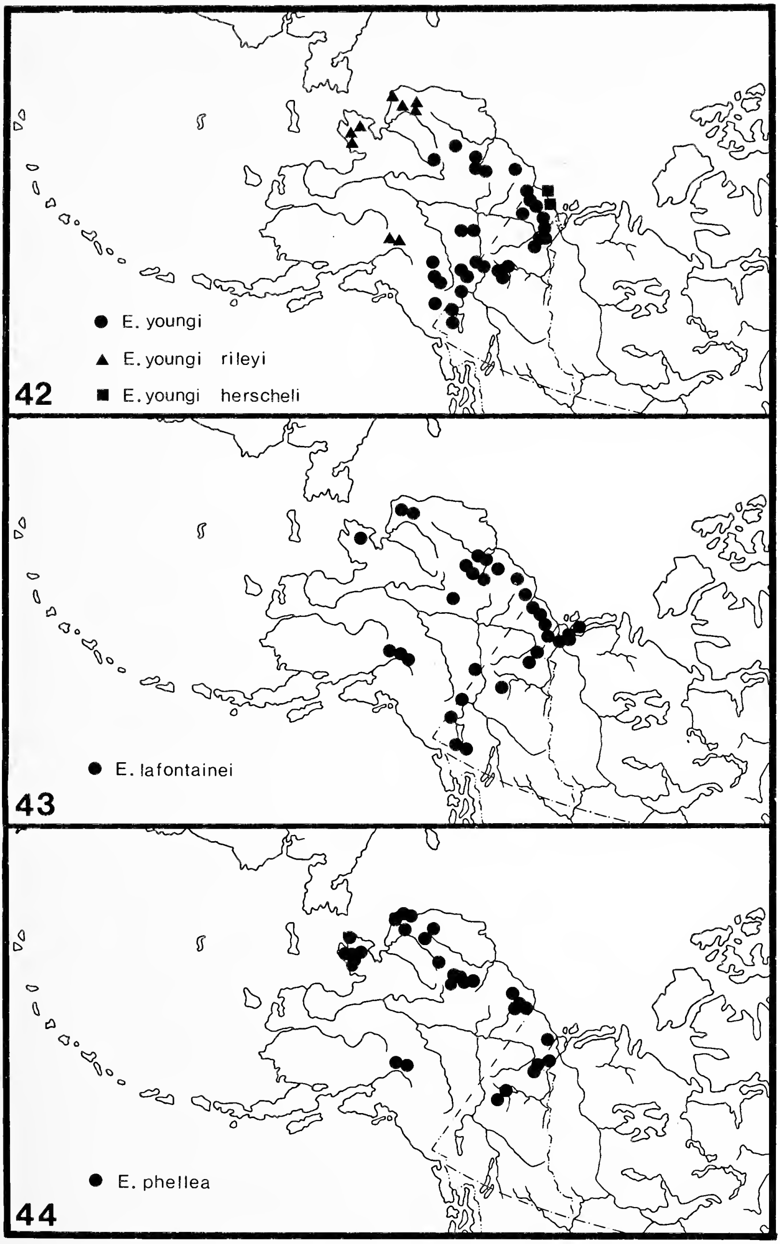
It is interesting to note that dos Passos (1972) determined the *E. youngi* lectotype to be dissimilar to *E. dabanensis* but the *E. youngi rileyi* holotype to be *E. dabanensis*. These determinations were made on the basis of genital characters only. Although not stated in that paper, the only character which could have led dos Passos to that conclusion is the coarser spines on the valva of the *E. youngi rileyi* holotype. The spines on the valva of *E. dabanensis* are very coarse and well separated; however, those of *E. youngi* can be coarse, fine, or anything in between. The tip of the valva of *E. youngi* is never narrowed and pointed to the same degree as that of *E. dabanensis*. Our examination of the *E. youngi rileyi* holotype has revealed that this specimen has nothing to do with *E. dabanensis* and is hereby placed as a subspecies of *E. youngi* (once again).

Although the *E. youngi rileyi* holotype (Figs. 9, 10, 46c) is *E. youngi*, the type series is mixed. We examined the holotype, allotype, and 23 paratypes. The holotype and seven paratypes are *E. youngi rileyi*, the allotype and five paratypes are *E. phellea*, and 11 paratypes are *E. lafontainei*. Dos Passos (1947, p. 3) states that "From the eight dissections of *youngi*, no positive conclusions can be drawn. There is considerable variation among specimens from the same locality." The reason that there was considerable variation among specimens from the same locality is that dos Passos was looking at three distinct species, and the variation within each of those three species is not that great at all.

Given this confusion, it is surprising that so many of the characters by which dos Passos differentiated *E. youngi rileyi* from *E. youngi youngi* are valid differences. Only two characters given by dos Passos (1947) are invalid in separating these two subspecies: *E. youngi rileyi* usually has black pupils in the forewing ocelli, they are not often absent as suggested by dos Passos; and *E. youngi rileyi* (FW length 21.5 ± 1.1 mm) is not smaller than *E. youngi youngi* (FW length 20.2 ± 1.1 mm), although specimens from the Seward Peninsula and Cape Thompson Areas are slightly smaller than those from Denali Park. Both of these erroneous differences are more diagnostic of *E. phellea* and must not be associated with *E. youngi rileyi.*

### **Erebia phellea** Philip & Troubridge, **new species**

**Description. Male:** (Figs. 25, 26, 37 & 38) mean alar expanse 36.1 ± 2.0 mm (N = 20, TL), range 31.8-39.0 mm. **Forewing**: mean length 19.1 ± 1.0 mm (N = 20, TL), range 16.1-20.2 mm. (Note: Richardson Mts.: FW mean length 21.2 ± 1.2 mm (N = 20)). Bolshoi Annachag Range: FW length 22.1 ± 0.9 mm (N = 20). **Dorsal Forewing**: ground color dark brown with four ochre-red to ochre-orange submarginal ocelli, usually containing minute black pupils (approx. 0.3 mm in expanse, up to 1.0 mm in Siberian specimens) in cells, $M_1$, $M_2$, $M_3$, and $CU_1$. The anterior two pupils usually noticeably larger than the posterior pair, and sometimes the entire ocellus shows similar size differences. In flight, freshly emerged males show a faint bluish, almost iridescent, sheen. Fringe generally concolorous with wing, but somewhat lighter at base of fringe forming an indistinct paler band parallel to and just beyond margin of wing membrane. **Dorsal Hindwing**: ground color dark brown, slightly darker towards wing base, with three to five small (to about 0.8 mm in most



Figs. 42-44. (42) distribution of *E. youngi* and its subspecies in North America; (43) distribution of *E. lafontainei* in North America; (44) distribution of *E. phellea* in North America.

specimens, occasionally to about 1.5 mm) ochre-red to ochre-orange submarginal ocelli, usually containing minute (to about 0.25 mm in most specimens, occasionally to 0.5 mm, and up to 1 mm in a few Siberian specimens) black pupils. Some Siberian specimens lack HW ocelli. Fringe concolorous with wing, with less tendency than FW to have a post-membranal lighter band. **Ventral Forewing**: ground color dark brown, very lightly suffused with dark rust-brown scales, and sometimes a postmedian-submarginal orange flush. Four ochraceous submarginal ocelli correspond with those present on dorsal surface. These ocelli have small black pupils, again with the anterior pair usually larger than the posterior pair. Fringe generally concolorous with wing, but again with a post-membranal lighter band. **Ventral Hindwing**: hairs white to creamy tan (light brown in Siberian specimens), giving wing obscure dark gray cast. Ground color of entire wing dark brown to blackish brown with a light suffusion of rust-brown and light pearl gray scales (gray scales lacking in most Siberian material, giving wing a sooty look) across entire wing, slightly heavier in postbasal and submarginal areas; an obscure, crenulate mesial band is edged by slightly darker brown bands (the band barely visible in may specimens); submarginal ochraceous ocelli with black pupils correspond with those present on dorsal surface (ocelli lacking in some Siberian specimens); marginal band absent except in some individuals from the Alaska Range, and about half of the specimens from the Magadanskaya Oblast'; fringe concolorous with wing.

**Male Genitalia**: (Figs. 50, 51a-51c, 52-55) mean length of costa of valva (distance "A" in Fig. 58) 1.83 ± 0.09 mm, range 1.83-1.97 mm (N = 20). Valva with short, wide neck and long tapered tip. Raised ridge at distal end of valva with many fine spines scattered in no particular order or number along costal margin of ridge and down slope to neck, usually stopping at neck but occasionally extending onto neck for a short distance. Raised, spined portion of valva 67.2 ± 2.5%, range 62-72% (N = 20) of entire length of costal margin of valva (see Fig. 58). Distal edges of vertical processes of aedeagus sheath usually fairly straight, although this is not a reliable character.

**Antenna**: (Fig. 39) medial side of antenna club very dark brown as illustrated, usually with light ochre median line. Dark brown on either side of median line may be reduced to equal sized patches of dark brown on upper and lower halves of nudum within each segment. Size of these patches variable in different specimens, but top half never darker than lower half.

**Female**: (Figs. 27, 28, 30, 32, 37, 38) mean alar expanse 36.9 ± 1.2 mm (N = 15, TL), range 34.1-39.0 mm. **Forewing**: mean length 18.9 ± 0.7 mm (N = 15, TL). (Note: Richardson Mts. mean length 21.3 mm (N = 3). Bolshoi Annachag Range: FW length 21.6 ± 0.47 mm (N = 8)). **Dorsal Forewing**: ground color paler than male, submarginal ocelli ochre-yellow and often slightly larger than those of male. A dusting of white (Alaska/Canada material) or gray (Siberian material) scales at apex. Gray scales along anterior edge of costa. These white or gray scales produce a pearly sheen on the insect in flight. Fringe lighter than ground, checkered with darker brown at tips of veins (lightness and checkering most marked in western Alaska material, least marked in Magadanskaya Oblast' material). **Dorsal Hindwing**: as in male but lighter ground color. **Ventral Forewing**: ground color lighter than male. A pronounced submarginal ochre-red, ochre-yellow, or grayish brown band is present on most specimens, containing the ocelli which may or may not contrast with the band. The black pupils are usually larger than those on the dorsal surface. Fringe pale and checkered (Seward Peninsula and western Brooks Range) to concolorous and faintly checkered (northeastern, Alaska Range, and Magadanskaya Oblast' material). **Ventral Hindwing**: hairs white (western Alaska) to tan (northeastern and Alaska Range) to light brown (Magadanskaya Oblast'). General pattern as in male, but a heavy dusting of pearly gray scales presents (especially in western Alaska material) a pronounced hoary appearance (except Magadanskaya Oblast' material where the gray scales do not contrast as much with the ground color). Fringe as on VFW.

### Type Series

Holotype male: Alaska: Seward Peninsula, km 66-68 Council Rd., 9-11 km NNE of Solomon (64.63N, 164.37 W), 60-180 m, 29 VI 1971 (D. G. Roseneau) in the National Museum of Natural History, Washington, D.C., U.S.A.

Paratypes, 471 males, 117 females:

N.W.T.: Richardson Mts.: Dempster Highway, km 491, 26 VI 1980 (J. D. Lafontaine & D. M. Wood), 4 males and 2 females in the ALS, 9 males & 1 female in the CNC.

Yukon Territory: Richardson Mts.: Dempster Highway, km 465, 23-28 VI & 5-7 VII 1980 (J. D. Lafontaine & D. M. Wood), 2 males & 1 female in the ALS, 6 males in the CNC; Dempster Highway, km 416, 22-28 VI 1980 (J. D. Lafontaine & D. M. Wood), 2 males in the ALS, 1 male in the CNC; Dempster Highway, km 406, 19 VI 1981, (J. T. Troubridge), 3 males in the Troubridge collection. Ogilvie Mts.: Dempster Highway, km 155, 18-20 VI 1980 (J. D. Lafontaine & D. M. Wood), 1 male in the ALS; Dempster Highway, North Fork Pass, 12 & 20 VI 1962, (R. E. Leech & P. J. Skitsko), 2 males in the CNC; Dempster Highway, km 140, 1-4 VII 1973 (D. M. Wood), 1 male in the ALS.

Alaska: NW Coast: Cape Lisburne, 8 VII 1977, (A. Springer), 11 males & 2 females in the ALS; Saligvik Ridge, Ogotoruk Valley (near Cape Thompson), 7-19 VII 1977, (K. W. Philip), 17 males & 5 females in the ALS. North Slope: Utukok R., 13 km SW and 14.5 km SSW junction with Carbon Creek, 25 VI-4 VII 1974, (K. W. Philip), 67 males (1 dep. J. Zeligs) & 15 females in the ALS; Noluck Lake, 1-6 VII 1972, (K. W.

Philip & C. Parker), 4 males & 3 females in the ALS. Brooks Range: DeLong Mts.: Wulik Peaks, head of Kivalina River, 13 VII 1974, (K. W. Philip), 1 male in the ALS. Western Brooks Range: Akuliak Lake, 8 km NE of Howard Pass, 3 VII 1981, (J. Zeligs), 1 male in the ALS, 1 male in the Troubridge collection. Brooks Range: Endicott Mts.: Nanushuk Lake, 8 VII 1971, (J. L. Harry), 1 male in the ALS; Kollutuk Mt., 8 km SSW Anaktuvuk Pass, 20 VII 1971, (J. L. Harry), 1 male in the ALS; Rumbling Mt., 8 km ESE Anaktuvuk Pass, 21 VI 1971, (J. L. Harry), 1 male in the ALS; VABM Yenituk, 22.5 km SW Anaktuvuk Pass, 23-27 VI 1971, (J. L. Harry), 6 males & 3 females in the ALS; 5 km SW of Atigun Pass, 6 VII 1979, (D. Faulkner), 2 males in the ALS; N side Atigun Gorge, 14 VII 1979, (J. Shepard), 1 male in the ALS; ridge 5 km N of N end of Galbraith Lake, 9 VII 1979 (K. W. Philip), 1 female in the ALS. Brooks Range: Franklin Mts.: Lake Schrader, hill between Spawning Ck. & Sadlerochit R., 8 VII 1973, (K. W. Philip), 1 female in the ALS; E. side Lake Peters, 1 VII 1973, (C. Batten), 1 male in the ALS; Whistler Ck., W of Lake Peters, 8 VII 1973, (C. Batten), 2 males & 1 female in the ALS. Brooks Range: British Mts.: Kongakut River, 5 km N of Paulaluk River, 7 VII 1975, (R. Ritchie), 2 males & 1 female in the ALS. Brooks Range: Davidson mts.: headwaters of Sheenjek River, 16 VI 1975, (C. Batten), 1 male in the ALS. Seward Peninsula: Tin City, 19 VII 1977, (D. A. Woodby), 1 male in the ALS; N fork Kougarok River, 3 km ESE Harris Dome, 1-2 VII 1971, (K. W. Philip & D. G. Roseneau), 25 males & 7 females in the ALS; head of Willow Creek (trib. of Penny River) nr km 22.5 Teller Rd., 14 VI 1970, (D. G. Roseneau), 5 males & 1 female in the ALS; W. side of Sinuk River, 6.5 km above Teller Road bridge, 8 VI 1970, (D. G. Roseneau), 1 male in the ALS; km 29 Teller Road, 13 VI & 5 VII 1970, (D. G. Roseneau), 5 males & 2 females in the ALS, 24 VI 1971, (D. G. Roseneau & A. Springer), 4 males in the ALS, 4-5 VII 1971, (K. W. Philip & A. Springer), 7 males & 5 females in the ALS, 21 VII 1976, (K. W. Philip & D. P. Oosting), 4 males & 3 females in the ALS, 30 VI & 13 VII 1980, (C. S. Guppy), 87 males & 9 females in the Guppy collection; km 34 Teller Road, 22 VII 1976, (K. W. Philip & D. P. Oosting), 3 males in the ALS, 22 VI 1980, (C. S. Guppy), 5 males & 1 female in the Guppy collection; Wheel Creek (trib. Penny River), 2 VII 1971, (D. G. Roseneau), 1 male in the ALS, 21 VI 1980, (C. S. Guppy), 4 males & 1 female in the Guppy collection; km 82 Kougarok Road, 17 VII 1980, (C. S. Guppy), 2 males & 1 female in the Guppy collection; km 64.5 Kougarok Road, head of Star Creek, 29 VII 1980, (C. S. Guppy), 1 female in the Guppy collection; 3 km N of km 58 Kougarok Road, 16 VII 1980, (C. S. Guppy), 20 males & 10 females in the Guppy collection; km 51.5-53 Kougarok Road, 4 VII 1980, (C. S. Guppy), 1 male in the Guppy collection; km 45 Kougarok Road, 8 & 18 VII 1980, (C. S. Guppy), 98 males & 18 females in the Guppy collection; km 42 Kougarok Road, 10 VII 1980, (C. S. Guppy), 12 males & 3 females in the Guppy collection; km 66-68 Council Rd., 9-11 km NNE Solomon, 19 VI 1970, (D. G. Roseneau), 1 male in the ALS, 12 VI 1971, (W. L. Foster), 4 males & 2 females in the ALS, 29 VI 1971, (D. G. Roseneau, A. Springer, & W. Walker), 27 males & 13 females in the ALS, 15-16 VII 1979, (J. Zeligs), 1 male & 1 female in the ALS, 2 males & 1 female in the Troubridge collection. Alaska Range: Denali National Park: Cathedral Mt., 25 VI 1972, (P. Pyne), 1 female in the ALS, Teklanika River, 2.5 km SSE Teklanika Campground, 14 VI 1972, (T. Bundtzen), 1 male in the ALS. Rampart House (?): North Creek, no date or collector, 1 female in the NMNH. (Note: There are three "North Creeks" listed in Orth's Dictionary of Alaska Place Names (1967)). One is in the Aleutian Islands, and may be neglected. One is on the Seward Peninsula N of Teller, an area from which we know of no butterfly specimens in any museum collection. The third is in the Talkeetna Mts., near Palmer, where some collecting was done in the early 1900's. There are other specimens of rockslide species in the NMNH labelled "Rampart House, North Creek, Alaska (Barnes coll.)," and since this specimen has a "Barnes coll." label, its most probable location is Rampart House, Alaska/Yukon border.

The total number in the type series is 589 specimens. Samples of the Alaska paratypes will be deposited in the CNC, NMNH, the Troubridge collection, and the Zoological Institute, Academy of Sciences, Leningrad, U.S.S.R.

## Distribution and Habitat

(Figs. 44 & 45) *Erebia phellea* is found in suitable scree and blockfield habitats from the Richardson Mts. of the N.W.T., west and south through the British Mts. and Ogilvie Mts. of the Yukon, west throughout the Brooks Range in Alaska, the Seward Peninsula, and in the Alaska Range (Denali National Park). One locality for the species has been found in the Magadanskaya Oblast', U.S.S.R., in the Bolshoi Annachag Range, upper Kolyma River. Aside from that locality, nothing is known about this species' distribution in NE Siberia, but further collecting in the many mountain ranges in Chukotka and the western Magadanskaya Oblast' may yield additional localities.

*Erebia phellea* is a denizen of dry, rocky habitats, preferring gravel to heavier block scree. Through much of its range it is found flying with *Clossiana distincta* (Gibson, 1920), and *Erebia magdalena mackinleyensis* (Gunder, 1932)—but if any given site has well-demarcated areas of block and gravel scree, then *E. phellea* will usually be restricted to the gravel, while the other two rockslide species will be found in greatest abundance on the blocks. The flight period for *E. phellea* is mid-June to late July, with emergence at approximately the same time as *E. lafontainei* and about two weeks before *E. youngi.*

## Diagnosis

*Erebia phellea* is characterized externally by its very obscure ventral hindwing, which has no obvious marginal band (except individuals from Denali National Park, Alaska; and approximately half of the specimens from the single locality in the Magadanskaya Oblast') and has a very indistinct mesial band in most specimens; by the four ochre forewing ocelli which have very tiny (but up to 1 mm in some Magadanskaya Oblast' specimens) or absent black pupils; by the antenna which has an equal amount of dark brown on either side of a pale ochre median line along the medial side; and by the hairs on the ventral wing surfaces which are whitish or tan, never red. Internally, *E. phellea* is characterized by the male valva which is long and pointed, has a wide neck, many very small teeth extending across the costa of the comb, thence down to the neck of the valva; and by the raised comb which occupies 62-72% of the entire length of the costa of the valva.

## Remarks

*Erebia phellea* exhibits a large degree of geographic variation over its 3500 km east-west range. Specimens from the Richardson Mts., eastern Brooks Range, and the Ogilvie Mts. (Figs. 29 & 30) differ from those from the Seward Peninsula and western Brooks Range as follows: the northeastern populations have a larger size (about 2.5 mm greater FW length), pupils in the dorsal ochre-red submarginal ocelli which are smaller or more often absent, and a wide submarginal red patch usually present on the ventral forewing (a feature which is present on some western Alaska specimens but with decreasing frequency towards the Seward Peninsula). Specimens from the Alaska Range (Figs. 31 & 32) most closely approach the northeastern populations but will often have more distinct marginal and mesial bands on the ventral hindwing. Specimens from the Bolshoi Annachag Range (Fig. 38) are even larger than the Richardson Mts. specimens (about 3.3 mm larger than the western Alaska specimens), have larger black pupils in the forewing ocelli than any North American populations (up to 1 mm in diameter), a narrow submarginal band on the ventral forewing in about half of the specimens, and faint but unmistakable marginal bands on the ventral hindwing (again, in about half the individuals). Ecologically, the Bolshoi Annachag Range is not dissimilar to the Alaska Range foothills in Denali National Park, so the appearance of a marginal VHW band in both these populations is possibly an indication of environmental similarities.

The variation from the Richardson Mts. to the Seward Peninsula may not suggest naming the extremes as subspecies, since various characters (as: FW length, VFW submarginal band, color of ocelli, hoariness of female VHW, etc.) do not correlate well. The Magadanskaya Oblast' material is distinct enough that it would have been separated immediately as a subspecies had it been discovered in the early days of northern collecting—but we hesitate to describe it in the face of our total ignorance about the variation of this species (if any) from Chukotka to the Kolyma River. A clinal intergrade to Seward Peninsula material is possible, and further collecting in the Magadanskaya Oblast' is needed before any meaningful subspecific assignments can be made.

*Erebia phellea* can be separated from all other species of the *E. dabanensis* complex by the antenna, wing, and genital characters given in the key. In addition, the spines on the ridge of the male valva of *E. phellea* are more numerous and much finer than those of *E. youngi*, *E. dabanensis*, and *E. lafontainei*.

*Erebia phellea* is most closely related to *E. dabanensis* and *E. youngi* (see Fig. 59), but remains distinct in every part of its range. Nowhere have we seen specimens which could be considered intermediate between *E. phellea* and any other species of the *E. dabanensis* complex, and species status is therefore warranted. We name this new species *E. phellea*, *phelleus* from Greek, meaning stoney ground.

Warren (1930) described *E. kozhantshikovi* ab. *rubescens* from one specimen from the Sayan Mountains, and in 1936 redescribed it as *E. dabanensis* ab. *rubescens*, giving figures of facies (pl. 84, figs. 1176 & 1182) and genitalia (pl. 42, fig. 384). Comparison of Warren's figures with specimens of *E. phellea* from the Aborigen Station suggests a strong possibility that *E. phellea* may fly in the Sayan Mountains, although we hesitate to draw firm conclusions from a single specimen which the authors have not examined. The name *rubescens* is unavailable for this taxon because it was described as an aberration and is an unavailable infrasubspecific name.

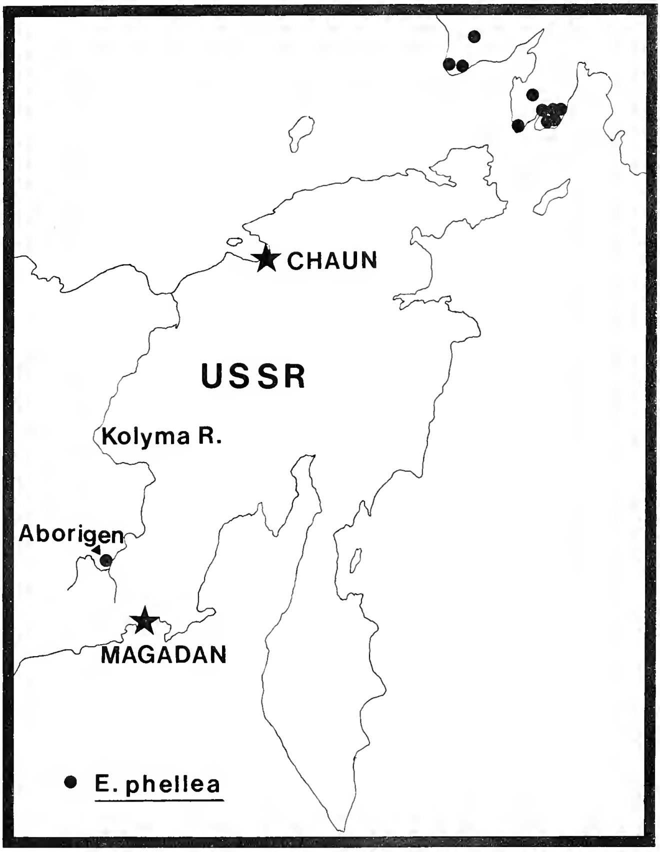
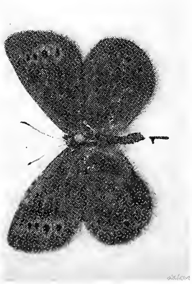


Fig. 45. Distribution of *E. phellea* in Eastern Siberia.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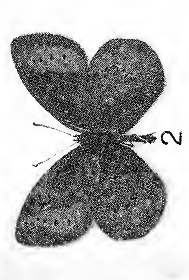
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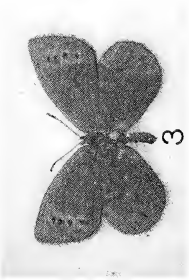
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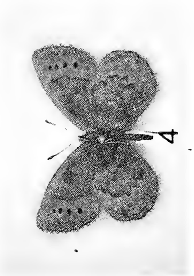
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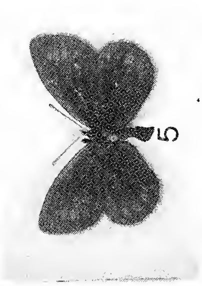
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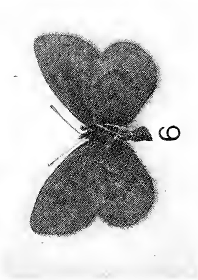
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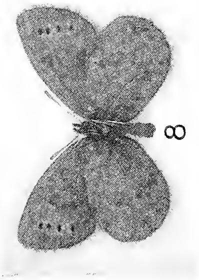
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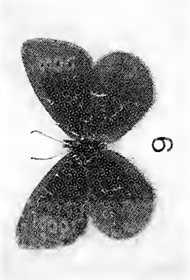
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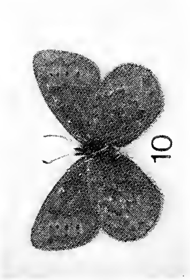
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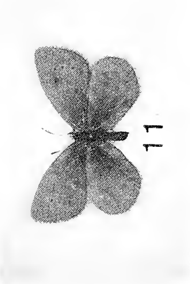
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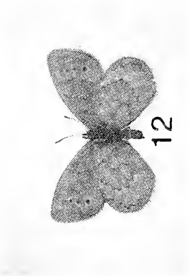
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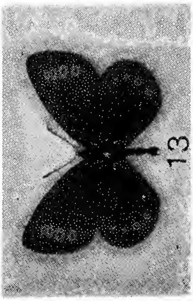
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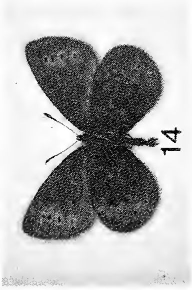
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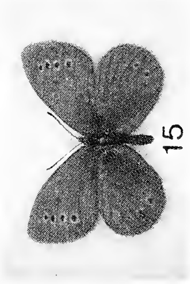
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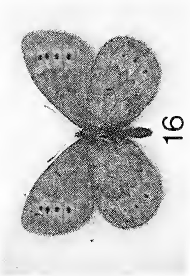
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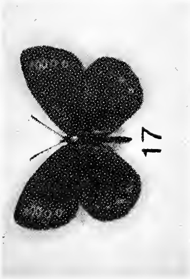
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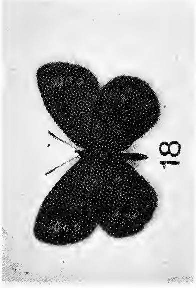
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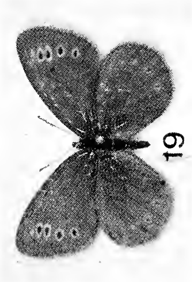
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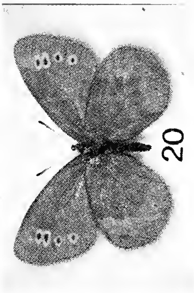
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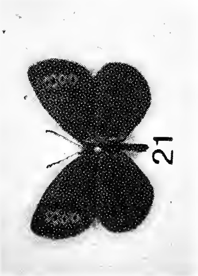
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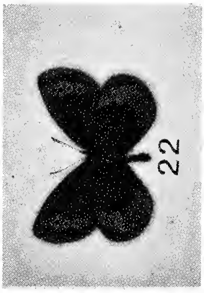
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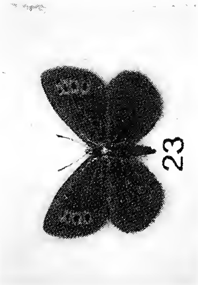
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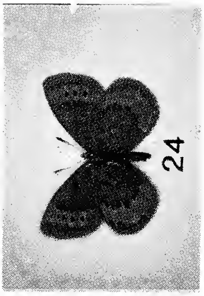
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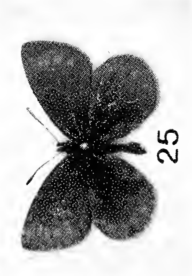
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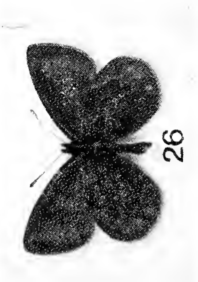
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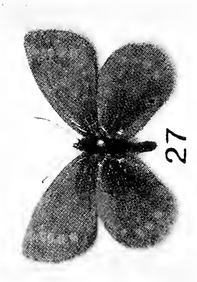
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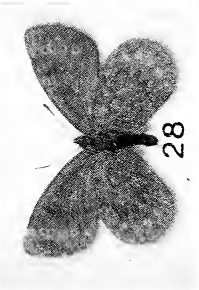
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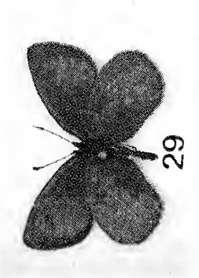
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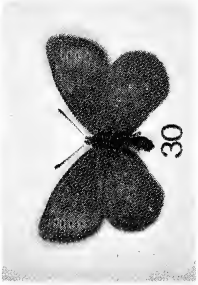
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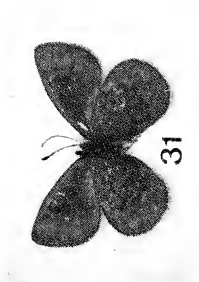
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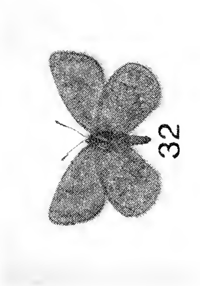
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Figs. 1-4. *E. youngi youngi*: (1) male, dorsal view; (2) male, ventral view; (3) female, dorsal view; (4) female, ventral view, all from Windy Pass, Ogilvie Mts., Yukon, 16 VI 1981, J. Troubridge Leg.

Figs. 5-8. *E. youngi herscheli*: (5) male, dorsal view; (6) male, ventral view; (7) female, dorsal view; (8) female, ventral view, all from Herschel Island, Yukon, 23 VII 1953, C. D. Bird, Leg.

Figs. 9-12. *E. youngi rileyi*: (9) holotype male, dorsal view; (10) holotype male, ventral view; (11) paratype female, dorsal view; (12) paratype female, ventral view, all from McKinley Park, Alaska, 19-20 VI 1932.

Figs. 13-16. *E. dabanensis*: (13) male, dorsal view; (14) male, ventral view, both from E. side Pik Vlastnyi, S.E. end Range Bolshoi Annachag, Magadanskaya Oblast', U.S.S.R., 15 VII 1980, K. W. Philip Leg.; (15) female, dorsal view; (16) female, ventral view, both from Chulugaischa, Mondy Sajan Mont, Buryat Republic, U.S.S.R., 2300 m, late June, 1926.

Figs. 17-20. *E. kozhantshikovi*: (17) male, dorsal view; (18) male, ventral view; (19) female, dorsal view; (20) female, ventral view, all from E. side Pik Vlastnyi, S.E. end Range Bolshoi Annachag, Magadanskaya Oblast', U.S.S.R., 28-30 VI 1978, K. W. Philip, Leg.

Figs. 21-24. *E. lafontainei*: (21) holotype male, dorsal view; (22) holotype male, ventral view; (23) paratype female, dorsal view; (24) paratype female, ventral view, all from N. slope Mt. Decoeli, St. Elias Mts., Yukon, 1300 m, 27 VI 1982, J. Troubridge & L. Lang, Leg.

Figs. 25-32. *E. phellea*: (25) holotype male, dorsal view; (26) holotype male, ventral view; (27) paratype female, dorsal view; (28) paratype female, ventral view, all from km 62, Council Rd., Seward Peninsula, Alaska, 29 VI-4 VII 1971, D. G. Roseneau, Leg.;(29) male, ventral view; (30) female, ventral view, both from km 416, Dempster Hwy., Richardson Mts., Yukon, 22-28 VI 1980, J. D. Lafontaine & D. M. Wood, Leg.;(31) male, ventral view; (32) female, ventral view, both from McKinley Park, Alaska, 20 VI 1932.

## **Erebia kozhantshikovi** Sheljuzhko, 1925

### Diagnosis

Forewing length of male 20.6 ± 0.6 mm, range 19.0-22.4 mm (N = 20) (Note: 10 of these specimens from Bolshoi Annachag Range, Magadanskaya Oblast', and 10 specimens from Sredne-Kolmysk, Province Yakutsk, NE Siberia).

*Erebia kozhantshikovi* (Figs. 17-20, 36) is characterized externally by the dorsal forewing ocelli, which usually are five in number (all other species of the *E. dabanensis* complex normally have four DFW ocelli) and contain distally pointed elliptical black pupils similar to those of *E. lafontainei* and *E. youngi*; by the dorsal hindwing, whose submarginal ocelli are larger and more numerous than those of *E. lafontainei, E. youngi,* and *E. phellea*, and have black pupils (dark brown in *E. lafontainei*); by the ventral forewing, which has a submarginal row of fulvous ocelli which are reduced to narrow halos around large black pupils (never coalesced to form a submarginal fulvous band as in *E. dabanensis, E. youngi,* and less frequently, *E. lafontainei*); by the ventral hindwing, which has a heavy scattering of pearl-white scales within cell $M_2$ of the postmedian-submarginal band, becoming very heavy toward and along the mesial band within this cell; by the medial side of the antenna club (nudum), which has a dark brown median patch (see Fig. 40) as in *E. lafontainei*; and by the fringe of the female which is rarely checkered with dark brown at the tips of the veins (fringe never checkered in *E. lafontainei*).

Internally, *E. kozhantshikovi* is characterized by the male valva (Figs. 49 & 57) whose spines are very fine as in *E. phellea* (never coarse as in *E. dabanensis* and *E. lafontainei*); by the spined ridge of the valva which occupies 50.1 ± 3.4% of the entire length of the costa (a smaller proportion than those of *E. phellea, E. dabanensis*, and *E. lafontainei*, a greater proportion than that of *E. youngi*), and is not usually elevated above the neck of the valva to the same degree as those of the other four species within this complex; and by the vertical processes at the distal end of the aedeagus sheath, which are usually greatly concave as in those of *E. lafontainei* (not usually flat or slightly concave as in *E. dabanensis, E. phellea*, and *E. youngi*).

## Distribution and Habitat

*Erebia kozhantshikovi* ranges from the 120th meridian (Yablonoi Mts., Vilui and Olenek Rivers) to the Magadanskaya Oblast'. Kurentzov places it along the north coast of the Sea of Okhotsk from about 140 to 155 degrees east, and mentions a published record for northern Korea, but Kurentzov's determinations in this group are suspect until his material is re-examined. K. Philip found *E. kozhantshikovi* flying in mixed larch/deciduous forest at the Aborigen Station, Magadanskaya Oblast', U.S.S.R. (very abundant in 1978, somewhat rare in 1980). K. Philip and E. A. Makarchenko collected this species at the Chaun Station (base of Chaun Gulf, Chukotka, 170 degrees east) in 1978, in lush tundra meadow/shrub tundra. The ALS collection has material (from Soviet volunteer collectors) from the Detrin River, Jack London Lake, Stokovoye (all in the Okhotsk-Kolyma Uplands), and Kremyanka (30-40 km west of Ust' Chaun). The ALS also has one specimen of *E. kozhantshikovi* from the Indigirka River, Yakutia, which had been determined by its collector as *E. tundra* (presumably from the erroneous genitalia figures in Kurentzov (1970)).

The flight period of *E. kozhantshikovi* is mid-June to mid-July.

Type locality: Dzhugdzhur Mountains at the headwaters of the Dzhelinda River, U.S.S.R.

## **Erebia tundra** Staudinger, 1887

### Remarks

No diagnosis is possible, since we have no access to material of this taxon. Whatever its status, *E. tundra* should be mentioned here, since it is listed as a species occurring in the Magadanskaya Oblast' in Korshunov's catalogue (1972), and also in Kurentzov (1970).

and Kurentzov (1970) also treats it as a species and states that *E. tundra* and *E. dabanensis* are allopatric species in the Magadanskaya Oblast', with *E. tundra* being the more northern and eastern in distribution. We have seen figures of the valva of *E. tundra* (Chapman, 1898, p. XV, figs. 51x a & b) and have seen a color figure of the type (Staudinger, 1887). From this information, we concur with Warren (1936) in that *E. tundra* is probably conspecific with *E. dabanensis*.

Kurentzov's figures for the genitalia of *E. tundra* and *E. dabanensis* match Warren's (1936) figure of *E. kozhantshikovi*, and vice versa. Kurentzov's key (using wing facies only) to *Erebia* appears inconsistent for these three taxa, and it is therefore not possible to decide what Kurentzov meant by the name "*E. tundra*". We should also mention that Chapman's figures of the genitalia of *E. dabanensis* (1898, pl. XV, figs. 51b & c) do not fit our concept of *E. dabanensis* and are probably assignable to *E. kozhantshikovi* (as pointed out in Warren (1936)).

We received one specimen attributed to *E. tundra* from Dr. Elena Antonova (Zoological Museum, Moscow University), which on dissection proved to be *E. kozhantshikovi* (see Fig. 56). We are thus reduced to noting the occurrence of the name "*E. tundra*" in the recent Russian literature, without being able to decide which of the *E. dabanensis* complex species is being referred to. Our best estimate is that a northern population of *E. kozhantshikovi* is currently being assigned the name "*E. tundra*" by Russian lepidopterists.

## **Erebia lafontainei** Troubridge & Philip, **new species**

**Description. Male:** (Figs. 21, 22, 35) mean alar expanse 36.9 ± 1.7 mm (N = 20, TL) range 33.5-40.0 mm. **Dorsal Forewing:** mean length 20.1 ± 1.0 mm (N = 20), range 18.0-22.3 mm. Ground color dark brown with four fulvous submaginal ocelli with black pupils in cells $M_1$, $M_2$, $M_3$, and $CU_1$. These pupils oval or elliptical with narrowest end on the distal side. Fringe concolorous with wing. **Dorsal Hindwing:** ground color dark brown with zero to four dull, fulvous submarginal ocelli. These ocelli usually very small (mean width 0.6 mm) with dark brown pupils absent, although ocelli may reach 1.5 mm in width and rarely have dark brown pupils (never black). Fringe concolorous with wing. **Ventral Forewing:** hairs red. Basal area gray-brown with very heavy suffusion of bright rust-red scales, extending distally to slightly darker postmedian line. Submarginal band of light gray-brown suffused with rust-red scales contains single fulvous ocelli in cells $M_1$, $M_2$, $M_3$, and $CU_1$. These submarginal ocelli may coalesce to form a submarginal band and extend into anterior portion of cell $CU_2$ in occasional specimens. These ocelli have single black pupils. Crenulate marginal band dark gray-brown basally, light gray-brown distally, and heavily suffused with bright rust-red scales. White scales absent in apical area. Fringe concolorous with wing. **Ventral Hindwing**: hairs red. Basal area dark brown, heavily suffused with rust-red scales; postbasal band gray-brown with light suffusion of rust-red scales and very light scattering of grayish white scales near submedian band; base of mesial band medium to dark brown, heavily suffused with rust-red scales, curved distally within discal cell; centre of mesial band gray-brown, heavily suffused with bright rust-red scales, pearl-white scales absent; outer edge of mesial band medium to dark brown, heavily suffused with rust-red scales, curved inward along each vein (and again mid-way through each cell to a lesser degree in many specimens); postmedian-submarginal band light gray-brown, very heavily suffused with pearlescent pink and light rust scales; submarginal fulvous ocelli correspond with those, if present, on dorsal surface; marginal band light gray-brown, very heavily suffused with bright rust-red scales and scalloped inward between veins; veins within marginal band edged with slate-gray scales; fringe concolorous with marginal band. The ventral hindwing has an overall smooth, reddish-brown or maroon appearance, due to the absence of white scales which would produce a hoary appearance, and due to the light gray-brown ground color which does not overpower the effect produced by the suffusion of rust-red scales.

**Male Genitalia**: (Fig. 48) mean length of costa of valva (distance "A" in Fig. 58) 1.64 ± 0.07 mm, range 1.57-1.77 mm (N = 20). Valva with raised ridge at tip with many coarse spines scattered in no particular order or number along costal margin of ridge. Raised, spined portion of valva 54.3 ± 2.0%, range 50-59% (N = 20) of entire length of costal margin of valva (distance "B" in Fig. 58). Distal edges of vertical processes of aedeagus sheath usually greatly concave, although this is not a reliable character.

**Antenna**: (Fig. 40) medial side of antenna club (the side which faces the other antenna) light ochre along dorsal and ventral margins with dark brown to light brown patch centrally located and tapering to a point toward posterior end of club. This dark patch is rarely faded to obscurity. Caution is advised in examining dried specimens for antenna characters, as medial side of club (nudum) could be mis-located, depending on how the antenna dried.

**Female**: (Figs. 23, 24, 35) mean alar expanse 37.4 ± 1.7 mm, range 35.0-40.5 mm (N = 20, TL). **Dorsal Forewing and Hindwing**: mean length of forewing 20.7 ± 0.9 mm, range 19.0-22.5 mm (N = 20). As in the male but ground color slightly lighter brown. Fringe concolorous with wing, checkering at tips of veins absent. **Ventral Forewing:** as in that of male but hairs orange-red and submarginal band and basal areas suffused with orange-rust scales, which produces ligher overall appearance than that of male. **Ventral Hindwing:** hairs red; basal area gray-brown, heavily suffused with light rust scales; postbasal band pinkish to buff, lightly suffused with light rust scales; base of mesial band medium brown, heavily suffused with light rust scales, curved slightly outward within discal cell; centre of mesial band light brown, heavily suffused with light rust scales; outer edge of mesial band medium brown, heavily suffused with light rust scales and scalloped as in that of male; postmedian-submarginal band light gray-brown, heavily suffused with light rust scales; submarginal ocelli correspond with those, if present, on dorsal surface; marginal band as in that of male but suffusion of rust scales more orange than red. Fringe as in forewing.

## Type Series

Holotype male: Yukon: St. Elias Mts., Mt. Decoeli, 1300 m, 27 VI 1982 (J. T. Troubridge & L. E. Lang), in the Canadian National Collection (CNC), Ottawa, Ontario, Canada.

Paratypes, 223 males, 83 females:

N.W.T.: Tuktoyaktuk, 21 miles (34 km) E, 20-25 VI 1971, (D. M. Wood), 6 males & 1 female in the CNC; Reindeer Depot, 1-10 VII 1948, (W. J. Brown & J. R. Vokeroth), 14 males & 6 females in the CNC; Richardson Mts., SW of Aklavik, 2-6 VII 1955, (C. Wyatt), 5 males in the American Museum of Natural History (AMNH); Inuvik, 7-10 VII 1982, (Q. Hess), 4 males & 7 females in the Troubridge collection.

Yukon Territory: St. Elias Mts., Mt. Decoeli, N slope, 1229-1384 m, 27 VI-2 VII 1982, (K. W. Philip), 21 males and 10 females in the Alaska Lepidoptera Survey collection (ALS), (Troubridge & Lang), 37 males & 6 females in the CNC, 36 males & 21 females in the Troubridge collection; St. Elias Mts., Nickel Creek, 1300 m, 3-6 VII 1982, (Philip), 6 males in the ALS, (Troubridge & Lang), 10 males & 8 females in the Troubridge Collection; St. Elias Mts., Bear Creek Pass, 30 VI-1 VII 1976, (C. S. Guppy), 6 males & 5 females in the Guppy collection; St. Elias Mts., Kluane Lake, S end, 28 VII 1974, (D. Scovell), one pair in the Scovell collection; Dempster Highway, km 416, 26 VI 1969, (Troubridge), 1 male in the Troubridge collection; Dempster Highway, km 83, 23 VI 1979, (Troubridge), 1 female in the Troubridge collection; Dempster Highway, km 90, 14 VI 1981 (Troubridge), 1 male in the Troubridge collection; Firth River; 13-17 VII 1976, (R. E. Leech & E. F. Cashman), 7 males & 1 female in the CNC; Dempster Highway, km 465, 23-25 VI 1980, (J. D. Lafontaine & D. M. Wood), 1 male in the CNC.

Alaska: Dalton Highway, km 97-110, hills N of Sagwon, 8-9 VII 1979, (F. & J. Preston), 5 males in the Troubridge collection, 4 males in the Preston collection; N ridge of Atigun Gorge, 13-14 VII 1979, (F. & J. Preston), 2 males in the Preston collection; Kivalina River, 14 VII 1974, (Philip), 2 males & 1 female in the

Troubridge collection, 1 male in the ALS; Utukok River, 24 VI 1974, (Philip), 2 pair in the Troubridge collection, 4 males & 1 female in the ALS; Itigaknit Mtn., 3 VII 1976, (Philip), 1 male in the Troubridge collection, 29 VI 1976, (D. Oosting), 1 male in the Jim Scott collection; 3 km ESE Harris Dome, 1 VII 1972, (Philip), 4 males & 3 females in the Troubridge collection; Anaktuvuk Pass, 13-15 VII 1970, (Philip), 4 males & 1 female in the AMNH; Okpilik Lake, 11 km NNE Mt. Michelson, 28 VI 1958, (Wm. Malcolm), 1 male in the AMNH; Umiat, 8-13 VII 1952, (G. W. Rawson & P. F. Bellinger), 10 males & 4 females in the CNC, 2 males in the James Scott collection, 6 VII 1959, (R. Madge), 1 male in the CNC, 5 VII 1959, (E. H. Martin), 1 male in the CNC; McKinley National Park (now Denali National Park), Highway Pass, 18 VII 1976, (Guppy), 2 males in the Guppy collection; McKinley Park, 17 VI-10 VII 1932, (ex. dos Passos coll.), 9 males (including 1 *E. youngi rileyi* paratype) in the AMNH, 5-6 VII 1938, (ex. Engelhardt coll.), 3 males (including 1 *E. youngi rileyi* paratype) in the AMNH, 7-15 VII 1930, (ex. Gunder coll.), 8 males & 4 females (including 8 *E. youngi rileyi* paratypes) in the AMNH.

The total number in the type series is 307 specimens. Samples of the Yukon paratypes will be deposited in the Carnegie Museum, the United States National Museum, and in the Zoological Institute, Academy of Sciences, Leningrad, U.S.S.R.

## Distribution and Habitat

*Erebia lafontainei* occurs from the Mackenzie delta of the N.W.T., west through the Richardson Mts., Ogilvie Mts., British Mts. and St. Elias Mts. of Yukon, the Alaska Range, Brooks Range, and North Slope of Alaska, to the Seward Peninsula. Although we have no record of its occurrence in British Columbia, it is found very near the British Columbia border in S. Yukon and may extend southward into that province (see Fig. 43).

*Erebia lafontainei* is a denizen of low shrub tundra, both arctic and alpine. Adults usually rest in the small patches of short sedge which are found between the low willows (*Salix niphoclada*, Rydberg, *S. lanata*, Linnaeus, *S. pulchra*, Chamisso) and birches (*Betula nana*, Linnaeus, *B. glandulosa*, Michaux) or in frost boils, where they are sheltered from the wind. Adults will often stray over fellfield or scree when their shrub tundra habitat comes in close contact with these other arctic biotopes.

The flight period is mid-June to late July, adults appearing on the wing one to two weeks ahead of *E. youngi* where they are sympatric.

## Diagnosis

*Erebia lafontainei* is characterized externally by the broad dark brown patch, centrally located on the medial side of the antenna club; by the reddish appearance of the ventral hindwing, which lacks white scales and never has a grizzled or hoary appearance; by the red hairs of the ventral surface; by the gray-brown ground color of the ventral hindwing (never dark brown) which does not overpower the influence of the scattering of red scales; by the fulvous patches of the ventral forewing which are usually reduced to a series of fulvous ocelli; and by the very small hindwing fulvous ocelli which usually lack pupils (however, when present are dark brown, not black). The female is further characterized by the lack of white scales within the marginal band at the tips of the veins, and by the fringe, which is never checkered with darker brown at the tips of the veins. Internally, *E. lafontainei* is characterized by the male valva, in which the spined ridge occupies 50-59% of the combined length of the toothed and untoothed portions of the costa. The pattern, length, proximity to one another, or number of spines must not be used in any attempt to separate *E. lafontainei* from *E. youngi* due to the individual variation exhibited by these characters (especially in the case of *E. youngi*). The above characters will separate *E. lafontainei* from *E. youngi* and *E. phellea*. Microscopic examination is required to determine the color of the pupils in the dorsal hindwing ocelli, the ground color of the ventral hindwing, and often to check the fringe of the female for checkering at the tips of the veins.

## Remarks

The geographic variation between populations of *E. lafontainei* is not extreme. Specimens which we have examined from the Seward Peninsula of Alaska agree well with those from the rest of its range in Alaska and northern Canada in internal and external characters. There is no evidence of a cline toward *E. kozhantshikovi* in western Alaska. Populations from the Richardson Mts., Ogilvie Mts., Mackenzie Delta, and Seward Peninsula tend to have fewer hindwing ocelli than those from the St. Elias Mts. and Alaska Range. Specimens from the North Slope and Seward Peninsula average slightly smaller than those from the other areas within its range. Neither of these character differences are significant enough to name a subspecies.

*Erebia lafontainei* can be separated from all other species of the *E. dabanensis* complex by the antenna, wing, and genital characters given in the key. In addition, *E. lafontainei* can be separated from *E. youngi* and *E. phellea* by the ground color of the ventral hindwing, which is gray-brown in *E. lafontainei* (dark brown to blackish brown in *E. youngi* and *E. phellea*). Unfortunately, microscopic examination is required to see the ventral hindwing ground color as it is obscured by the presence of rust-red scales in all three species.

*Erebia lafontainei* is most closely related to *E. kozhantshikovi* but remains distinct in every part of its range. Nowhere have we seen specimens which could be considered intermediate between *E. lafontainei* and any of the other species of the *E. dabanensis* complex, and species status is therefore warranted. We take pleasure in naming this new species in honor of J. Donald Lafontaine, who has freely given hours of his time to assist in this and other projects undertaken by the authors.

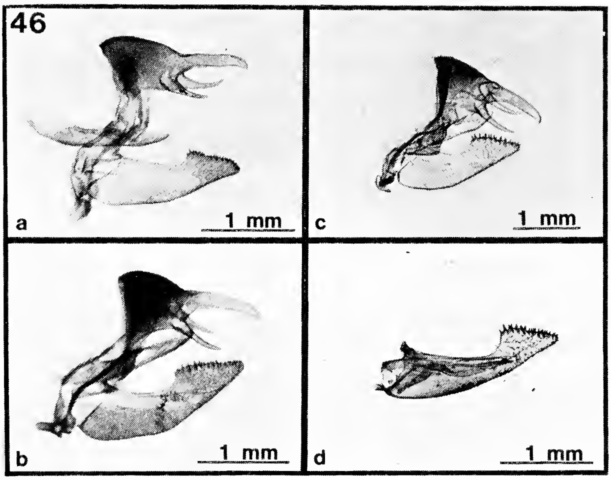


Fig. 46. Male genitalia of *E. youngi*, lateral view: (a) *E. youngi youngi*, Windy Pass, Ogilvie Mts., Yukon; (b) *E. youngi rileyi*, Ogotoruk Creek, Cape Thompson, Alaska; (c) *E. youngi rileyi* holotype, McKinley Park, Alaska, all with right valva removed and showing variation of tooth pattern and shape of valva; (d) right valva of *E. youngi herscheli*, inside view.

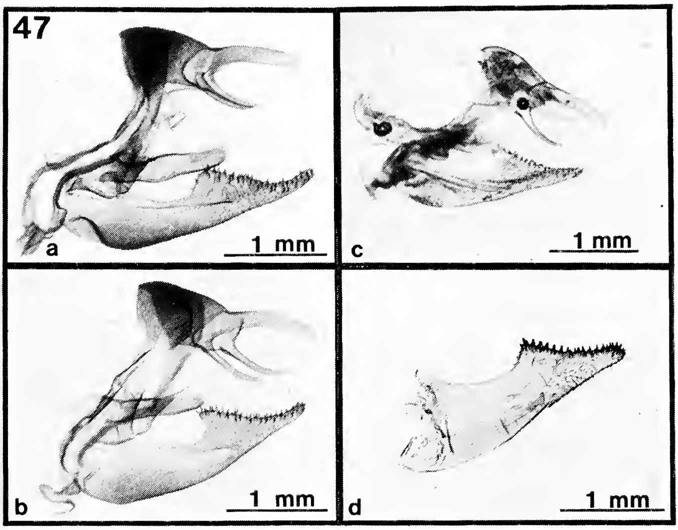


Fig. 47. Male genitalia of *E. dabanensis*, lateral view: (a-c) S.E. end Range Bolshoi Annachag, Magadanskaya Oblast', U.S.S.R., showing range of variation of male valva within a given population, the right valva has been removed for better viewing; (d) Chara Daban, Sajan Mont, Buryat Republic, 2000 m, inside view of right valva.

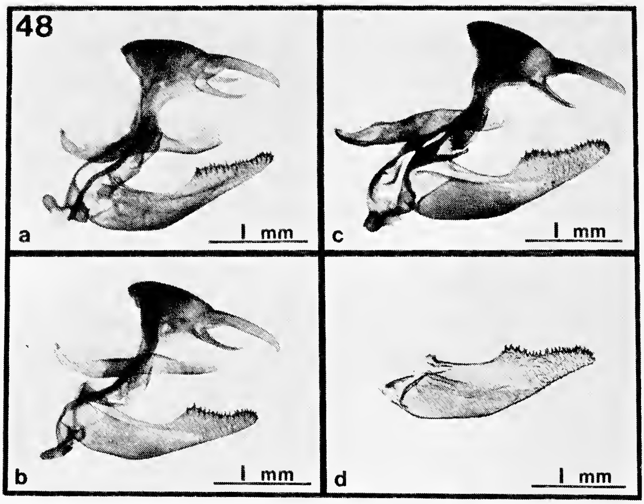
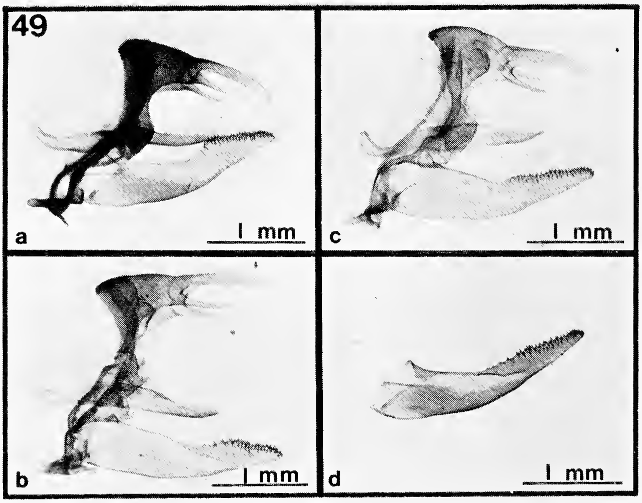


Fig. 48. Male genitalia of *E. lafontainei*, lateral view: (a & b) Harris Dome, Seward Peninsula, Alaska; (c) Inuvik, N.W.T., all with right valva removed, showing variation of valva shape; (d) Umiat, North Slope, Alaska, inside view of right valva.



Figs. 49. Male genitalia of *E. kozhantshikovi*, lateral view: (a & b) Sredne-Kolymsk, Province Yakutsk, N.E. Siberia, U.S.S.R., Lat 68°; (c) S.E. end Range Bolshoi Annachang, Magadanskaya Oblast', U.S.S.R., Lat 61°, all with right valva removed, showing range of variation in valva shape; (d) Range Bolshoi Annachag, Magadanskaya Oblast', U.S.S.R., inside view of right valva.

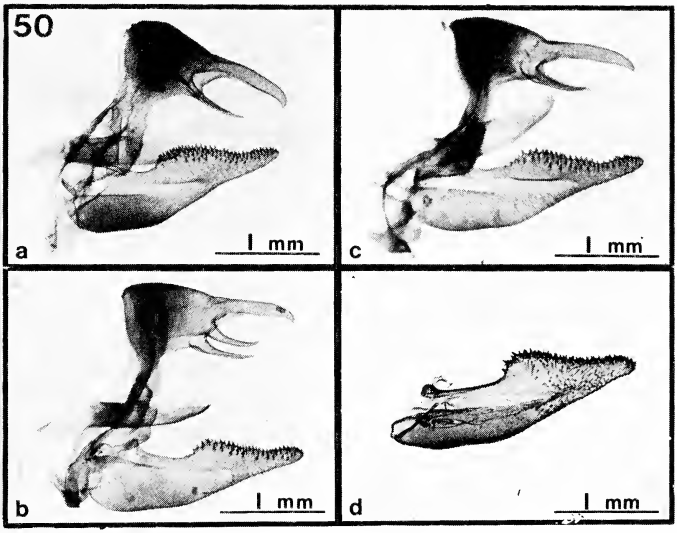


Fig. 50. Male genitalia of *E. phellea*, lateral view: (a-c) km 416-471, Dempster Hwy., Richardson Mts., Yukon, all with right valva removed, showing range of variation of tooth pattern and valva shape; (d) km 416, Dempster Hwy., Yukon, inside view of right valva.

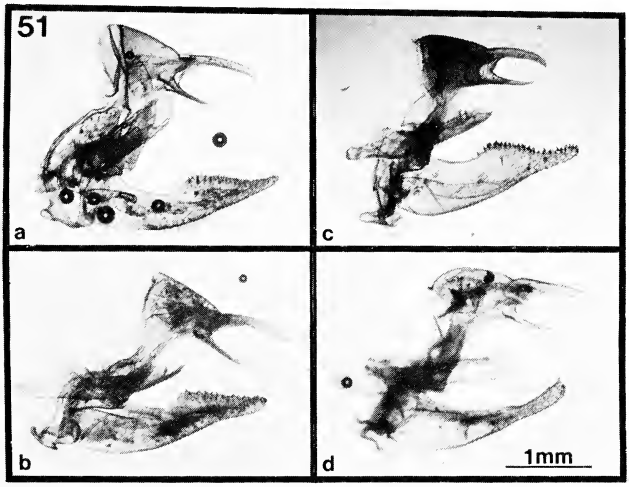
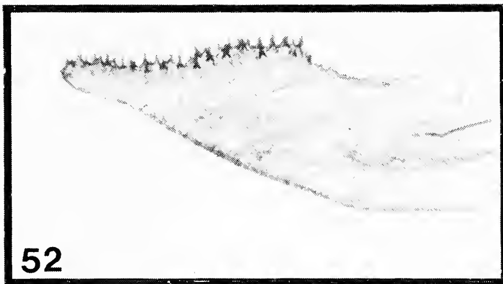


Fig. 51. Male genitalia of *E. phellea* and *E. fletcheri*: (a) *E. phellea*, (b) *E. phellea*, both lateral views from the Aborigen Station, Magadanskaya Oblast', 29 VI-5 VII 1980, A. C. Jones & K. W. Philip, Leg., (c) *E. phellea*, holotype, km 66-68 Council Rd., Seward Peninsula, Alaska, 29 VI 1971, D. G. Roseneau, Leg., (d) *E. fletcheri*, lateral view, Aborigen Station, Magadanskaya Oblast', 22 VI 1978, E. G. Matis, Leg.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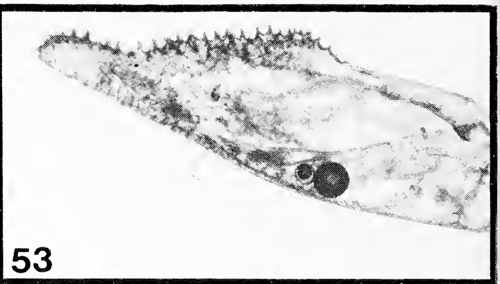
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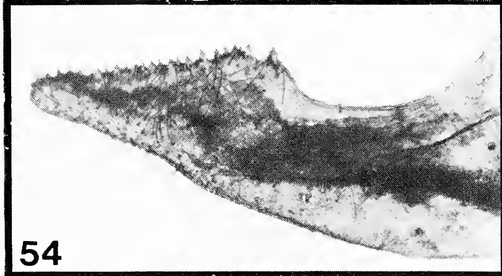
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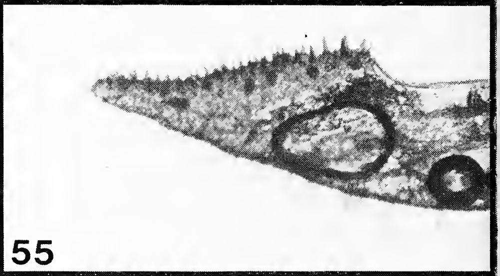
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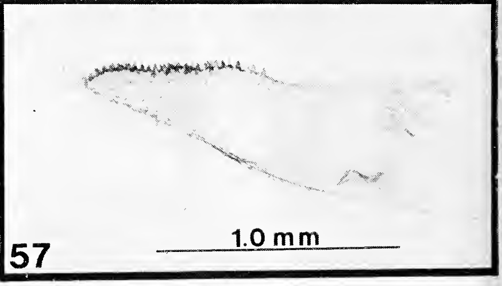
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Fig. 52. Valva of *E. phellea*, Utukok River, Alaska, 1 VII 1974, (K. Philip).

Fig. 53. Valva of *E. phellea*, Lake Peters, Alaska, 8 VII 1974, (C. Batten).

Fig. 54. Valva of *E. phellea*, Aborigen Station, Magadanskaya Oblast', 5 VII 1980, (K. W. Philip).

Fig. 55. Valva of *E. phellea*, same data as Fig. 54.

Fig. 56. Valva of *E. kozhantshikovi*, Indigirka River at mouth of In'yali River, 16 VI 1976, V. Kovalev, Leg. (this specimen had been previously determined to be *E. tundra*).

Fig. 57. Valva of *E. kozhantshikovi*, Chaun, Chukotka, 25 VI-15 VII 1978, E. A. Makarchenko, Leg.

## EXCLUDED TAXA

### **Erebia inuitica** Wyatt, 1966

### Remarks

*Erebia inuitica* was named from one specimen, supposedly caught by an Eskimo boy on the north slope of the Endicott Mts. (Anaktuvuk Pass) in Alaska. Warren (1968) states that this specimen is closest to *E. christi* (Ratzer, 1890), and "had it been taken in the European Alps, one could scarcely have done other than to accept it as a race of *E. christi.*" However, *E. christi* has black forewing ocelli which *E. inuitica* lacks, so the wings and genitalia closely resemble those of *E. pharte* (Hubner, 1804). Warren's dissection of the holotype proved it to be a member of the *epiphron* group of the genus *Erebia* and not the *alberganus* group.

We have studied photographs of the genitalic dissection of *E. inuitica* (Warren, 1968 & 1981). The valva of *E. inuitica* is very narrow in the distal one third and has no raised comb. The spines on the valva are coarser, fewer, and further apart than those of *E. phellea*, (the only member of the *E. dabanensis* complex which could slightly resemble *E. inuitica*). We have tried rolling the valva of *E. phellea* to approximate the rolled valva of *E. inuitica*; however, from no angle does it approach that of the *E. inuitica* holotype. We have obtained color photographs of the *E. inuitica* holotype and have not seen Nearctic specimens of any species which could be confused with it. We have determined that *E. inuitica* is not conspecific with either of our new species.

Although it is possible that *E. inuitica* does exist in Alaska, we feel that *E. inuitica* may have been described from a mislabelled specimen of *E. christi* or *E. pharte* from the European Alps, and that until a further series is taken in Alaska, *E. inuitica*'s species status should remain dubious. Kenelm W. Philip's trip to Anaktuvuk Pass in 1970 failed to produce *E. inuitica*. Subsequent discussions with Roosevelt Paneak, who collected for Wyatt, revealed that although he could not remember catching any particular specimen, he did not collect far from the village site and always collected on low tundra areas, never near scree.

### **Erebia fletcheri** Elwes, 1899

### Remarks

Kurentzov (1970) put *E. fletcheri* as a race of *E. dabanensis*, and others have done the same as pointed out in Warren (1930). Externally, *E. fletcheri* closely approaches *E. dabanensis*, but the male genitalia of *E. fletcheri* are completely different from anything in the *alberganus* group.

K. Philip collected *E. fletcheri* flying together with *E. dabanensis* and *E. kozhantshikovi* at the Aborigen Station, Magadanskaya Oblast', in 1978 and 1980. These specimens match Warren's figures (1936) for that species except for having one rather than two terminal spines on the valva (see Fig. 51d).

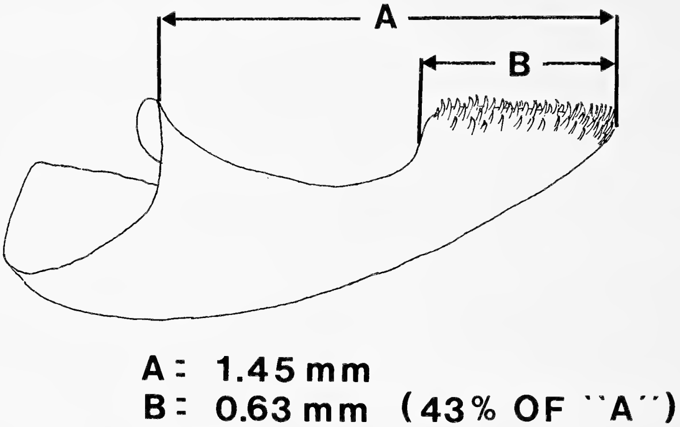

Fig. 58. Male valva of *E. youngi*, showing method used in its measurement. Distance "A" is measured from the point where the vertical process of the basal end meets the costa, to the tip. Distance "B" is measured from the tip, to a point mid-way down the shoulder of the spined ridge.

## Zoogeography

The *Erebia dabanensis* complex is chiefly Beringian. During the Wisconsin Glaciation, which reached its height about 20,000 years ago, the Cordilleran and Continental ice sheets of North American coalesced, effectively isolating much of northern Yukon and Alaska from the rest of North America. During this period, sea level fell by at least 115 meters, and the land bridge between Alaska and Siberia was restored. Although Alaska was isolated from central North America for 6,000 to 10,000 years, a vast area of tundra and grassland connected Siberia and Alaska. With the exception of large glaciers in the Koryak Mts., Anadyr Range, and Chukhotsk Peninsula, northeast Asia remained largely unglaciated. The repeated opening of dry land between Alaska and Chukotka during the various glacial advances may have allowed the ancestral forms of the *E. dabanensis* complex to move back and forth and speciate. With the end of the Wisconsin Glaciation came the final opening of the Bering Strait and the last time that endemic populations could have been genetically continuous with their ancestral forms.

In North America, *E. youngi*, *E. lafontainei*, and *E. phellea* have not extended their ranges more than a few hundred kilometers beyond the unglaciated areas of Alaska and Yukon. The very limited dispersal ability exhibited by these species is due to their weak flight capabilities, their very specific habitat requirements, and their short lifespans. We see no evidence of ancestral species of the *E. dabanensis* complex having survived Wisconsin ice in refugia south of Beringia. We know that many other arctic species were present in North America during the Sangamon Interglaciation (before Wisconsin ice), as many of these species survived the Wisconsin Glaciation in refugia located in Alberta and Colorado, as well as in Beringia (e.g. *E. magdalena, E. theano* Tauscher, 1809). As *E. youngi, E. phellea,* and *E. lafontainei* did not repopulate from the southern refugia after the retreat of Wisconsin ice, it is possible that their ancestral forms invaded North America from Siberia as recently as 20,000 years ago. However, it is also possible that these species survived the Illinoian Glaciation in Alaska and did not extend their ranges into central North America during the Sangamon period. Unfortunately, we have no way of knowing for certain where these species originated, we can only speculate.

## Ecological Separation of Species

In North America, *E. youngi, E. lafontainei,* and *E. phellea* are often sympatric. All three species fly together in the Richardson Mountains, Yukon, at the head of the Kivalina River (western Brooks Range), and at Harris Dome in the Seward Peninsula of Alaska. *Erebia youngi* and *E. lafontainei* fly together at the Utukok River (western Brooks Range), and at Nickel Creek (St. Elias Mts., Yukon), where the authors found good numbers of both species feeding together at the same mud puddles in 1982. We found *E. phellea* sympatric with *E. youngi* in many localities in the Richardson Mountains and Ogilvie Mountains of Yukon, and at many localities in the Seward Peninsula of Alaska. In each of these localities, *E. phellea* did not stray far from the scree, *E. youngi* did not stray far from the tundra meadow and fellfield, and *E. lafontainei* did not stray far from the low shrub tundra. It is not uncommon for all three of these habitats to be found in very close proximity to one another, and often all three will abut one another, especially in the low foothills of our arctic mountain ranges. In this situation, all three species may occur sympatrically, and ample opportunity for interbreeding occurs; however, we have seen no evidence of hybrids.

No real chronological separation of these species is evident in any part of their respective ranges. *Erebia lafontainei* and *E. phellea* usually appear on the wing one to two weeks before *E. youngi*, but both are on the wing throughout most of the flight period of *E. youngi*.

In the U.S.S.R., *E. kozhantshikovi* is found in mixed larch/deciduous forest as well as in areas of shrub tundra. It flies with *E. dabanensis* in the Bolshoi Annachag Range, Magadanskaya Oblast', in open larch bog habitats. At the Aborigen Station in the Bolshoi Annachag Range, *E. phellea* flies with *E. dabanensis* on very dry rocky spurs just above treeline, and is strictly limited to that habitat, although *E. dabanensis* is present from larch bog at 450 m to alpine tundra and fellfield at 1675 m.

## Discussion

There has been confusion among these *Erebia*, because all previous work on the *E. dabanensis* complex in North America was based on very few specimens, none of which were collected by the authors. Holland (1900) described *E. youngi* on the basis of four specimens collected by Rev. S. Hall Young in Eastern Alaska. The type series of both *E. youngi* and *E. youngi rileyi* contained specimens of our new species, as noted above. The authors have examined over 2,000 Nearctic and about 500 Palearctic specimens of the various species of this complex.

Warren (1969) was convinced that *E. youngi* and *E. dabanensis* occurred together in Alaska. In trying to distinguish between these two species, he states that "in *E. dabanensis* the length of the spined ridge is greater than that of the corresponding ridge of the proximal part; in *E. youngi* it is markedly shorter, in *E. dabanensis* the spines are coarse and well separated;. . . in *E. youngi* very fine and touching," and that "so far as available material goes, it is doubtful if *E. youngi* and *E. dabanensis* can be distinguished by their superficial appearance." Clearly, Warren was using only genital characters to separate *E. dabanensis* from *E. youngi*, placing specimens with coarse teeth and short comb as *E. youngi*. The result of this was the determination of all specimens of *E. youngi* with fine teeth on the valva as *E. youngi* and all specimens of *E. youngi* with coarse teeth (like the *E. youngi rileyi* holotype), all *E. lafontainei*, and all *E. phellea* as *E. dabanensis*. Although Warren clearly stated that the spined ridge on the valva of *E. dabanensis* is longer than the ridge of the neck of the valva, no attention was paid to this most important character when the *E. youngi rileyi* holotype was determined to be *E. dabanensis* (dos Passos, 1972). The spined ridge on the valva of the *E. youngi rileyi* holotype occupies only 43% of the entire length of the costa (Fig. 46c) and is not narrowed and pointed at the tip as we see in that of *E. dabanensis*.

Warren and dos Passos suggested that both *E. youngi* and *E. dabanensis* occurred in Alaska. We have demonstrated that this is not the case. The question which should have been asked is whether or not *E. dabanensis* and *E. youngi* are conspecific. Externally, *E. youngi* approaches *E. dabanensis* in every character in which it differs from *E. lafontainei*. Although slight differences in number, size, and shape of the submarginal ocelli do occur between *E. youngi* and *E. dabanensis*, one would find it difficult to pick a specimen of one out of a long series of the other without looking at the genitalia. The most significant structural difference between *E. youngi* and *E. dabanensis* is in the male valva; that of *E. dabanensis* with a much longer, more pointed and narrower tip than that of *E. youngi*, and the teeth on that of *E. dabanensis* being consistently coarse, whereas those of *E. youngi* are extremely variable and may be very fine to very coarse. These discrete differences in the male genitalia are consistent throughout the range of *E. youngi*, with no cline present between the Seward Peninsula or Cape Thompson, Alaska, populations and those of the Richardson Mountains, N.W.T. Similarly, we see no evidence of a cline between specimens of *E. dabanensis* which we have studied from the south end of Lake Baikal and the Magadanskaya Oblast', U.S.S.R., a distance of over 3200 km. Further collecting of *E. dabanensis* within the Chukhotsk Peninsula, U.S.S.R., is required before we can fully understand the geographic variation exhibited by *E. dabanensis*.

As *E. youngi* and *E. dabanensis* are separated by the Bering Strait and are therefore allopatric, there is no contact zone between them. However, the valva differences between them are well outside the range of variation we would expect to see between two subspecies. and are even greater than those between other species in the genus which are sympatric (e.g. *E. magdalena* and *E. fasciata* Buter, 1868). As *E. youngi* shows no evidence of a cline towards *E. dabanensis* in western Alaska, and *E. dabanensis* shows no evidence of a cline towards *E. youngi* from the Buryat Republic to the Magadanskaya Oblast', U.S.S.R., we do not hesitate to treat them as full and separate species.

*Erebia lafontainei* is very distinct from *E. dabanensis, E. phellea*, and *E. youngi*. While there is no doubt that three species of the *E. dabanensis* complex occur in North America, it is important to note that two of these species, *E. youngi* and *E. lafontainei*, are not most closely related to each other but have their most closely related counterparts in the U.S.S.R. It is of interest to note that in many external characters in which *E. lafontainei* differs from *E. dabanensis* and *E. youngi*, it approaches *E. kozhantshikovi*. The antenna club of *E. kozhantshikovi* is identical to that of *E. lafontainei*, the ventral hindwing of both species are reddish and neither appears grizzled or hoary, and the ochre submarginal band on the ventral forewing is usually reduced to a series of ocelli in both species. However, the hindwing maculation of *E. kozhantshikovi* is far more extreme than that of *E. lafontainei*, especially in that of the female, and the fringe of female *E. lafontainei* is concolorous with the wing but that of *E. kozhantshikovi* may be checkered with darker brown at the tips of the veins. Internally, we see significant differences in the valvae of these two species (Figs. 48, 49, 57). The spined ridge of *E. kozhantshikovi* is extremely variable in the percentage of the total length of the costa which it occupies; however, it averages shorter than that of *E. lafontainei* as indicated above. The spined ridge of *E. kozhantshikovi* is normally not elevated above the neck of the valva to the same degree as that of *E. lafontainei*, and the spines on that of *E. lafontainei* are much coarser than those of *E. kozhantshikovi*.

*Erebia lafontainei* and *E. kozhantshikovi* are completely allopatric; however, they are more different from each other than are *E. youngi* and *E.*

*dabanensis*. One would never have any difficulty in picking a specimen of *E. lafontainei* out of a long series of *E. kozhantshikovi* by facies alone, and similarly, a specimen of *E. kozhantshikovi* would not be lost in a lengthy series of *E. lafontainei*. As the differences between *E. lafontainei* and *E. kozhantshikovi* are as great, or greater than many species of *Erebia* which are sympatric (and species in this genus are separated by relatively small differences (e.g. *E. sudetica* Staudinger, 1861 and *E. melampus* Fuessli, 1775)), we do not hesitate to treat them as distinct species.

The geographic variation we see in *E. phellea* is extreme, as noted above. Specimens from the Bolshoi Annachag Range, Magadanskaya Oblast', differ from specimens from Alaska by their larger size, their slightly darker hairs on the ventral hindwing, their larger ocelli, and by the more distinct mesial and marginal bands on the ventral hindwing. Internally, the male genitalia are identical to those of the Alaska populations (see Figs. 51a-c, 52-55). Although there are slight size and wing differences between these two populations, these differences are not outside the range of variation which we expect to see between subspecies. Since the male genitalia and habitat preference, as well as antenna characters, and many wing characters are similar between these two populations, we treat them as being conspecific.

## Phylogeny of the *E. dabanensis* Complex

The cladogram shown in Fig. 59 illustrates our interpretation of the relationships among the species of the *E. dabanensis* complex, part of the *alberganus* group of Warren (1936). The *E. dabanensis* complex (lineage 1 of Fig. 59) has the following two character states that we consider derived: a crenulate VHW mesial band, and four submarginal forewing ocelli which lack white pupils. Members of lineage 2, consisting of *E. kozhantshikovi* and *E. lafontainei*, share the presence of a dark brown central patch on the medial surface of the antennal club, contrasting with the ochre dorsal and ventral surfaces. In lineage 3, to which belong *E. phellea, E. dabanensis* and *E. youngi*, the dark brown dorsal surface of the antennal club is sharply delineated from the ochre or brown ventral surface by a narrow ochre longitudinal line. Lineage 4, consisting of *E. dabanensis* and *E. youngi*, share the following character states: ground color of VHW dark brown; postbasal and postmedial areas of VHW with heavy scattering of white scales; angle between neck and apex of valva a right angle or less.

## Conclusions

Three closely related species within the *E. dabanensis* complex occur in North America. These Nearctic species are not most closely related to each other, but have their most closely related counterparts in the U.S.S.R. *Erebia youngi/E. dabanensis*, and *E. kozhantshikovi/E. lafon-*

*tainei* are two sets of sister species occurring on either side of the Bering Strait. Although *E. youngi* and *E. lafontainei* closely approach their U.S.S.R. counterparts, significant differences are found between them and we treat them as separate species. *Erebia phellea* occurs on both sides of the Bering Strait, and although there is a large amount of geographic variation throughout its range, we consider the Palearctic and Nearctic populations to be conspecific.

Although *E. dabanensis* and *E. kozhantshikovi* do not occur in North America, we have not seen specimens from Chukotka, and do not know the status of the complex in that region. It is possible that the Bering Strait does not form the western limit of the ranges of *E. youngi* or *E. lafontainei*.

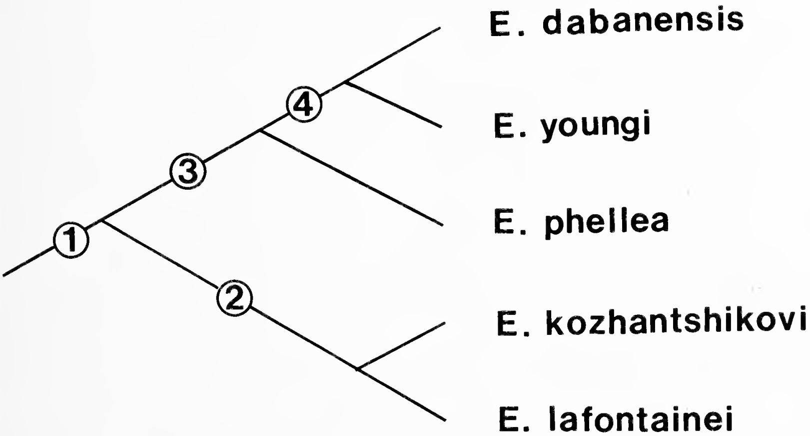

Fig. 59. Cladogram of the *Erebia dabanensis* complex.

*Acknowledgments.* We thank J. Donald Lafontaine, James A. Scott, David K. Parshall, D. M. Wood, and Joseph D. Zeligs for their help and advice. Dr. Lafontaine gave significant museum aid, while Dr. Scott assisted in characterizing the three North American species and in the preparation of the key. John E. Rawlins and the Carnegie Museum, Frederick H. Rindge and the American Museum of Natural History, Chris S. Guppy, and Douglas E. Scovell loaned specimens; Dr. Lafontaine and Dr. Scott reviewed the manuscript in its earlier stages and offered appreciated criticism, and the volunteer collectors of the Alaska Lepidoptera survey collected many of the types.

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# THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

*Volume 21* *Number 2* *Summer, 1982(83)*

## IN THIS ISSUE

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COVER ILLUSTRATION: Male genitalia of *E. lafontainei*, lateral view, Inuvik, N.W.T., with right valva removed, showing variation of valva shape. See Troubridge & Philip, page 136, this issue.

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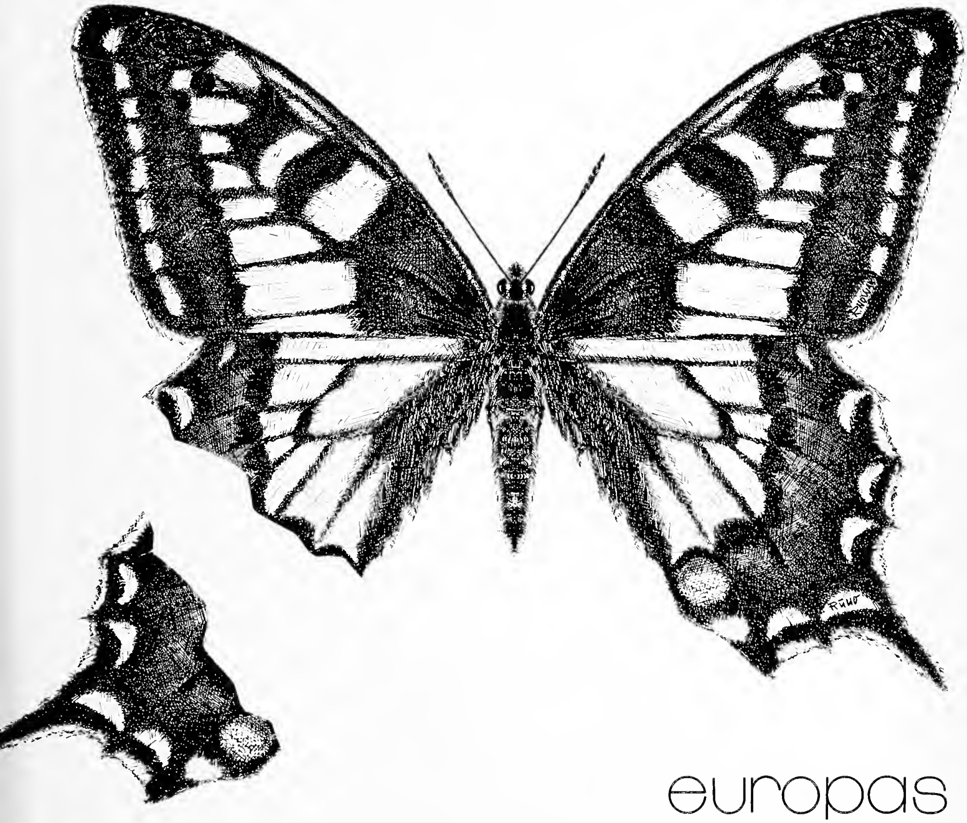

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*Journal of Research on the Lepidoptera* 21(3): 147-157, 1982(83)

# Plebeian Courtship Revisited: Studies on the Female-Produced Male Behavior-Eliciting Signals in *Lycaeides idas* Courtship (Lycaenidae)

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**Abstract.** The male courtship behavior of *Lycaeides idas* is described. It is shown that males search for mates among females perched in the vegetation with their wings folded. A specimen sitting in the resting position common to lycaenids, with its head facing the ground is more attractive to a male than one facing upwards, and it is suggested that the search image could be a specific pattern on the hindwing. The approach of males to blue objects, common in the lycaenids, is shown to be a behavior response unrelated to mate-search behavior. It is shown that an olfactory cue elicits the touch-down of the male beside the female.

## Introduction

The study of butterfly courtship behavior goes far back. The concept of behavior as a sequence of individually elicited steps, however, is of more recent date; the works of Tinbergen *et al.* (1942) and Magnus (1958) are milestones in this field.

In recent years a steady yet very thin stream of studies has been presented on the division of butterfly courtship behavior into separate phases. Numerous papers only treat the function of a certain sensual modality in the courtship, e.g., sight (Magnus, 1958; Lundgren, 1977) or smell (Bergstrom and Lundgren, 1973; Lundgren and Bergstrom, 1975) and thus only give a fraction of the sequence. More extensive attempts to track the importance of the different senses in the courtship behavior among the Lycaenidae have been presented by Douwes (1976a, b) for *Heodes virgaureae* (L.) and by Wago (1978) for *Zizeeria maha argia* (Men.).

The initiation of the present work arose from the studies of Lundgren (1977), published in this journal, where he demonstratd that *Plebejus argus* (L.) males show stronger response to females of the closely related *Lycaeides idas* (L.) than to their conspecifics. The males were presented the wing upperside of the females and the results were deduced to have originated from the males' attraction to blue color. Lundgren concluded that there must be another reproductive barrier to counteract this effect. This conclusion seems somewhat enigmatic: such a constant mistake by the male (i.e., always to prefer a nonsuitable mate) is energetically very expensive. A male who can differentiate some other way will have several advantages: he will not have to waste energy on extra searching within a non-rewarding category, and he is furthermore likely to find the proper mate before any of his less talented congeners. The increased fitness conferred on efficient males would predict that such male's offspring would flood the entire population within a few generations.

My observations and experiments concentrated on two questions. First, is the blue coloration of critical importance in the mate-search flight? Second, is there any indication that a possible female scent plays a part in the elicitation of (at least) part of the male courtship behavior?

## Materials and Methods

In the course of a study on the male androconial secretions of some plebejine species in 1978, I had the opportunity to observe the courtship behavior of both *L. idas* and *P. argus* repeatedly. Both species occurred sympatrically at a site on the island of Oland (southern Sweden; N56°42′ E16°31′). The locality is believed to be the one where Lundgren performed his experiments. The locality is a sandy pine-forested area. About half of the ground is covered by a dense mat of *Calluna vulgaris*. The flight period of *idas* began on July 5th, and lasted until August 1st. No extensive records were made in 1978.

In 1980 observations and experiments were performed at a locality in central Sweden, 18 km NNW of Orebro (N59° 25′ E15°04′). This locality (Figs. 1 & 2) consists of an artificially cleaned roadside. The vegetation consists mainly of *Calluna vulgaris* and a number of grasses. Surrounding areas are dry spruce forests and a pine-forested bog, respectively. At this locality *argus* was entirely absent. (Despite intensive sampling I never encountered *argus* in the area within the radius of one kilometer from the experimental site). In 1980 the first male *idas* was observed on July 11, and the first female on July 14. Bad weather conditions prevented systematic data gathering during much of the flight period, and only scant information on the courtship sequence could be added before July 28. The weather then improved and four days of intensive experimentation on the possible scent emission were possible. Beginning August 1 there was another 10 days of rain, during which only a few remaining specimens of both sexes were observed sitting in the vegetation, occasionally making short flights to forage on nearby flowers. After that no more specimens were seen that year.

The experiments were run between 1200-1600 hours for periods of about two hours each. The weather was relatively constant throughout the experimental period: approximately 22-25°C, wind velocity 2-5 m/s, degree of cloudiness 2/8-4/8 (mainly cumulus clouds).

In the experiments on the possible existence of female scents, two types of specimens were used: half of the specimens were freshly killed (never used for more than one hour *post mortem*), and half old specimens

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2

Fig. 1. The locality where the experiments were performed. The area was cleared a number of years ago; dense spruce forest on left, pine forested bog on right.

Fig. 2. Close up view of the experimental site. The track going from the chair and stones to the birch was a route frequently patrolled by males.

collected at the same locality in 1970 and 1971. All specimens had their wings tightly folded above the thorax in the usual resting position of blues (= the posture held by females courted successfully by males). All specimens were mounted on ordinary black insect pins, with the pin head only slightly above the thoracal surface so that it was not visible between the wings. Only female specimens were used in the experiments. In each experiment four specimens were pinned with their heads facing the ground on erect heather stems, in a spot known to be regularly routed by mate-searching males. This position in the vegetation is typical of resting *idas* females. In the experimental setup two of the specimens were freshly killed, and the other two were old ones. The specimens were arranged with specimens of the same age placed diagonally to each other at a distance of 15-20 cm to the nearest specimens. The specimens were moved one step counter-clockwise every ½ hour in order to nullify anomalies that might possible appear due to different visibility.

In another experimental series two old specimens were placed each with their heads facing upwards and downwards, respectively. This was done to determine the importance of orientation of the specimen.

Male courtship pattern was arbitrarily categorized into six phases depending upon the level of advance in the sequence at which it was ended. The division is by no means meant to represent an exact description of phases individually elicited; they are merely a means by which to quantify how far the crude steps had advanced. The phases were numbered 1-6, the key feature(s) of each phase is described below.

Phase 1: The patrolling/searching flight of the male is clearly arrested, and the male approaches to examine the specimen observed. Stronger expressions of this phase include fluttering around the specimen, whereas in some cases it becomes no more than a dip in the route flight.

Phase 2: The male flutters for several seconds around the specimen usually at the same level at which the object is situated. It does not,however, touch it.

Phase 3: The male flutters intensively around the specimen, frequently touching its counterpart with its wings. In the final stage the male tries to alight in close proximity to the female.

Phase 4: The male alights by the side of the female. Almost instantaneously he begins to vibrate his wings over the body plane very rapidly. Meanwhile he walks up to a position parallel to the length axis of the female.

Phase 5: The male bends his abdomen with its claspers extruded and widely apart, toward the genital region of the female. Often the fluttering behavior of the male continues throughout much of this phase.

Phase 6: The male clasps the female genitalia.

The response of all males that showed any of the steps described above were recorded. In cases where the male made subsequent approaches toward more than one dummy these were recorded as separate approaches. The response patterns achieved were statistically compared using the chi-square test for homogenuity with one degree of freedom at the 0.05 level of significance.

## Description of the Foraging and Mate-search Behavior of Males

Two major types of activity are easily recognizable in *idas* males: foraging and mate-search. When in the mate-search phase, the male performs a rather low, rapid, frequently interrupted flight. My observations indicate that they often follow routes along vegetational strips, e.g. along a border of heather at a roadside. These routes are patrolled for the entire period of mate-search flight, i.e., several hours. This behavior is dependent upon temperature and sunshine: whenever the temperature falls below ca 20°C and/or the sun is covered by clouds for a minute or more the behavior become interrupted and fragmentary. The males rest in the vegetation, and will only occasionally fly short distances, and then at very low speed. Often the behavior in such microclimatic changes will gradually change to foraging. An important characteristic of the latter is that the males almost completely lack the approach response to blue so heavily expressed while in the mate-search phase. The presence of strong attraction of males to blue coloration resulting in male-male interactions is a well-known phenomenon, but no case was found in the literature where emphasis has been put on the fact that this behavior only occurs in one "mood" of the male. However, in his dissertation, Robbins (1978) described a similar phenomenon among eumaeine hairstreaks.

When the butterflies forage they are often seen sitting in numbers on inflorescences, there being no aggressive tendencies. It should also be noted that it is during foraging the butterflies most frequently expose their wing upperside (Fig. 4). During the mate-search flight, however, males will approach any blue object present along or close to the route being patrolled (e.g., the author's blue jeans were an object thoroughly investigated by the male blues).

The first step toward courtship is the male seeking a proper mate. He does so by searching in the vegetation, where females sit quiescent on a stem. When a Lycaenid alights on a stem it immediately turns around so that it faces the ground. It is of importance to notice that all specimens sitting in this manner have their wings folded (Fig. 3). The upperside of the wings is not visible. Hence, it is not possible to distinguish the sexes by sight alone. Females that are found on flowers where they may be foraging or sunbathing (thermoregulating ?) frequently sit with their wings more or less open. They are often approached by mate-searching males, but always respond negatively under such circumstances (first bending the abdomen upwards, and if persistently courted, also vibrate their wings rapidly or escape).

After his initial approach, the male will perform at least parts of, sometimes the entire, courtship sequence. The extension of the courtship behavior of the male is completely dependent upon signals elicited by the female.

## Results

The total number of approaches as well as the number of courtships performed to a given level was higher for fresh specimens in all categories as shown by the data in Table 1. The difference is statistically significant in

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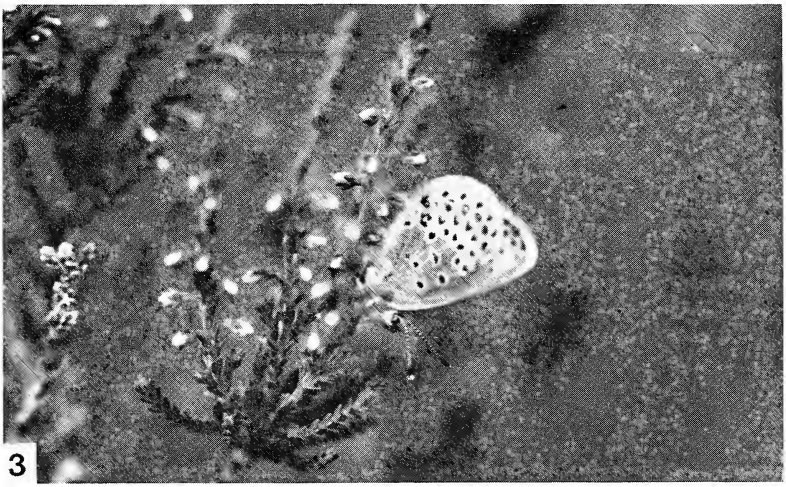

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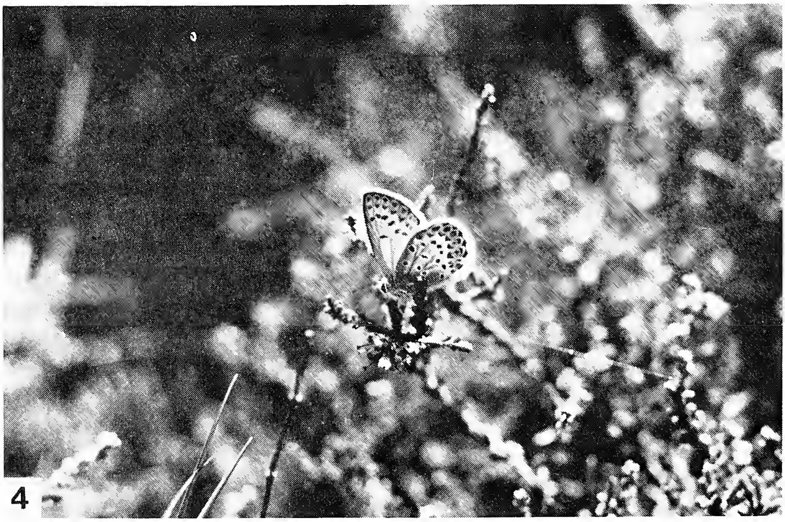

Fig. 3. Female sitting in resting posture on a heather stem.
Fig. 4. Male sitting in typical posture with wings apart, sunbathing.

TABLE 1. Behavioral responses of *L. idas* males to fresh and old female dummies. For further explanation see text.

| Phase<br>Dummy | 1 | 2 | 3 | 4 | 5 | 6 | Σ |
|---|---|---|---|---|---|---|---|
| F | 18 | 31 | 16 | 9 | 17 | 2 | 93 |
| O | 13 | 11 | 2 | 0 | 0 | 0 | 26 |
| $\chi^2$ | .81 | 9.52 | 5.44 | 9.00 | 17.00 | 2.00 | 37.22 |
| P | > .3 | < .005 | < .05 | < .005 | < .0005 | > 1 | <.0005 |

all cases except phase 1 (the initial approach). Analysis of the data shows that the difference in discrimination between the two types is strongest between phase 2 and 3. This indicates the point at which a crucial cue is lacking.

Observations on courtship established that the initial approach of the male is elicited by visual stimuli. It was hypothesized that the position of the resting lycaenids, to which group the receptive females belong, might be a part of the search image of the male. However, the experiments on this part of the study, with the dummies facing upwards or downwards, became fairly restricted as to the numbers recorded (due to weather conditions). From the values obtained for the total observations, Table 2, the preference for the specimen facing downwards is statistically significant at the 0.005 level.

## Discussion

The observations reported above on male behavior in the courtship of *L. idas* indicate that it is practically identical with the major sequences in other Lycaenids previously studied. [*Lycaeides argyrognomon* Brgstr. (Lundgren, 1977), *Zizeeria maha argia* (Wago, *et al.*, 1976; Wago, 1977, 1978), and *Heodes virgaureae* (Douwes 1976a, b)].

Wago *et al.* (1976) emphasized that males search for females sitting in vegetation with their wings folded. The fact that the males actually search for females with this presentation, and approach towards specimens sitting, e.g., on flowers with their wing uppersides well exposed to passing males, is an otherwise released behavioral response, will be shown below.

In his comprehensive studies on *Zizeeria maha*, Wago showed that the wing underside is visually similar in all parts of the visible spectrum. He showed that males approach dummies of both sexes at about the same frequency. Wago concluded that it is the color of the underside that elicits the primary approach towards the female. The undersides of the sexes of *idas* are visually indistinguishable to the human observer (they co-vary with respect to color). There is no reason to believe that there are differences in the visual attractiveness in any other part of the spectrum either, although this was not tested. Based upon the assumption, I excluded all male dummies from my experiments. The experiments did show that orientation is of utmost importance in the attractiveness of the resting insect. Those female dummies with their heads facing upwards did not provide the optimal visual signal, and consequently no responses after phase 1 were recorded. The specimen facing the ground elicited the complete visual stimulus phase 2, however, but did not possess the olfactory cue critical for the release of phase 3. Considering the fact that practically all receptive females are found in this latter position, such a finding is not surprising. Hence there is not only the question of wing color, as suggested for *Z. maha* by Wago *et al.* (l.c.), there must be a specific pattern recognition; be it the contours of the specimen, the position of the antennae, possibly some part of the hindwing pattern such as the row of bright-colored spots along the border, or some other feature. Whatever the case, the data suggest that the high level of specific discrimination among the males is a response entirely different from the very unspecific attraction to blue coloration. Such a "double entry" to a typical behavior is furthermore evolutionarily unlikely: as mentioned above, practically all receptive females sit in the resting posture. Females foraging on flowers or otherwise sitting with their wings exposed to the sun are practically

TABLE 2. The effect of age and resting position of female dummies on male behavioral responses of *L. idas*. F = fresh specimen, O = old specimen.

| Phase<br>Dummy | 1 | 2 | Σ |
|---|---|---|---|
| $F_1$ ↑ | 4 | 0 | 4 |
| $F_2$ ↑ | 2 | 0 | 2 |
| $O_1$ ↑ | 1 | 0 | 1 |
| $O_2$ ↓ | 4 | 11 | 15 |

| | | | |
|---|---|---|---|
| $\chi^2$ | .22 | 11.00 | 4.63 |
| P | > 50 | < .005 | < .05 |

already mated. A male wasting his time and energy on approach and courtship of such females would thus have a much lower fitness than his conspecific males searching for unmated females only. A strong selective pressure would be expected for the ability of males to search for mates among the folded-wing resting type only, as approaches toward open-wing females will not result in mating. The approach to blue coloration is a phenomenon of general occurrence among the blues as mentioned by Lundgren (1977). It deserves mention that in the case of *Plebicula dorylas* (Schiff.) the males do not approach the entirely brown upperside-exposing females, but retain the response to blue coloration as such (Pellmyr, unpubl.).

In one experiment Lundgren (1977) investigated female color preference by males of *P. argus*. In this experiment he used various combinations of dried and spread specimens of *idas* and *argus*. He measured the difference in approach to brown versus blue coloration. The results showed that the number of approaches were lowest for the mainly brown specimens, that it was significantly higher for the partially blue females, and even higher for the entirely blue males. The female of *argus* is on average much more brown than female *idas*, and in his experiments Lundgren consequently achieved a high number of cross-specific approaches. He concluded that there must be another factor responsible for the reproductive isolation than the color of the female wing upperside. When put in the light of the discoveries of Wago *et al.* (l.c.) and myself, the experimental design used by Lundgren was clearly inadequate for the measurement it was meant to produce. What he actually studied was the male's response to blue coloration. As shown above, this signal is completely different from that of the mate-search response eliciting stimulus. The parameter studied is of no importance in the courtship behavior, and could hence not be correctly considered among the possible reproductively isolating factors between *argus* and *idas*. Other cross-specific approach experiments would reveal the value of the initial visual signal as a specific recognition factor. In experiments with *Z. maha* and the closely related *Zizina otis* (F.) Wago (1977) showed that the males of *maha* responded equally well to the undersides of both species, and that the specific recognition factor hence must be another characteristic or response (e.g., some part of the female's response to the male's approach).

The approach to blue coloration and the first phase of the male courtship are superficially similar, but the evidence presented of their different initiation indicates that minor dissimilarities may occur when inspected more closely.

My experiments on fresh versus old females clearly indicate a difference in their attractiveness to the approaching males. Several of the sensory abilities that may differ between the two categories can be ruled out: thus tactile as well as visual are similar in both categories, but the existence of an olfactory cue seems to be confirmed by these results. Further, the results show that the first two phases are elicited at about the same rate for both old and fresh females (Table 1). The step from phase 2 to phase 3 appears as the step in the courtship behavior wherein the difference between the fresh and old specimens becomes significant. It should be noted, that both of the approaches that elicited phase 3 toward old females were recorded from males previously excited by persistent approaches toward fresh dummies (approach values for these = 5) a few seconds earlier. The major step in the interval between phase 2 and 3 is touchdown of the male beside the female. It is thus suggested that touchdown is the primary response elicited by the olfactory cue of the female. The origin and nature of the female scent is unknown. No identifiable scent scales are present on the wings of the female. Preliminary gas chromatographic analyses of female *idas* wings revealed a complete absence of volatile compounds (Bergstrom & Pellmyr, unpubl.). It is thus believed that the source is located somewhere on the body, possibly the abdominal glands. In both cases where the male coupled the dead female in the experiments I only separated them using brute force. Doing this the female's genitalia were drawn out due to the very obstinate grip of the male, and they were therefore cut off before further experimentation. At first encounter the male had no problem whatsoever to move up and couple with the female, but after the genitalectomy the male would search for a suitable grasp on many sites on the female in vain (e.g., at the costa). The same thing happened with all subsequent courting males. The intensity of their courting remained unaltered, and the longest courtship ever seen was actually recorded for one of these males: 5.5 minutes. Male sense of orientation toward the abdominal tip, however, was completely lost.

From his experiments on *Heodes virgaureae*, Douwes (1976b) concluded that an olfactory cue was present either on the forewings or on the thorax.

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*Journal of Research on the Lepidoptera* 21(3): 158, 1982(83)

## Parallel Albinism in Two Theclines (Lycaenidae)

*Stryomon melinus* (Huebner) occasionally develops an aberration in which the normally orange-red "*thecla* spot" in cell $Cu_2$ on both surfaces of the hindwing is straw yellow. This aberration has been called *meinersi* Gunder, although such name, of course, has no taxonomic standing. I recently published a color illustration of a *meinersi* specimen (Holland, 1980[1981]. Aberrant New Mexican butterflies. J. Res. Lepid. 19(2):88-95).

A research request by Mr. Ted Pike of Fairview, Alberta, Canada, for *Harkenclenus titus* (Fab.) material caused me to photograph my New Mexican examples of this species. Much to my surprise, I discovered that the normally coral submarginal spots (including the *thecla* spot) were nearly pure white on one specimen. This albinis and a typical New Mexican *titus* specimen are illustrated in Figures 1 and 2, respectively. *H. titus* males normally have no coral markings dorsally, and thus there is no way this aberration could find expression on that wing surface.

*H. titus* is not common in New Mexico, except in the northern tier of counties. During 93 days of collecting over 21 years in the Sacramento Mountains, it was encountered only once: at that time, 3♂♂ and 1♀ were taken including the illustrated aberration. These four specimens were found at the summit of 10,000′ Nogal Peak. It is believed, due to the presence of both sexes, however, that specimens were not hilltopping to seek mates. Rather, I speculate that only a very tiny area around the summit was high enough to provide the requisite habitat for *H. titus* this far south in New Mexico. (There are no New Mexican records for *H. titus* either south or west of Nogal Peak.) If this assumption is correct, it is possible that the Nogal Peak colony of *H. titus* is very small, and may have a significant fraction of its individuals with a recessive allele producing this partial albinism.

Notably, the tip of the antenna club in the aberrant specimen is a normal coral color. In *meinersi* aberrations of *S. melinus*, the tip of the antenna club is also normally colored. An analogous allele may therefore produce the partial albinism in both theclines. Moreover, the antenna tip color, although normally the same as the coral *thecla* spot, is apparently controlled from a different set of genetic loci.

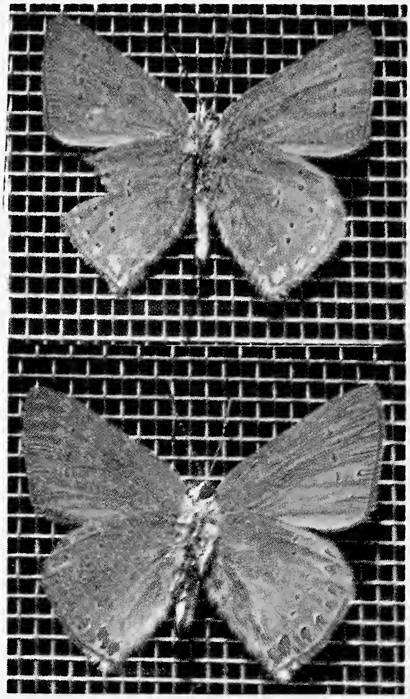

Fig. 1. *Harkenclenus titus* aberrant ♂, 9 Aug. 1975, Nogal Peak, Sacramento Mts., Lincoln Co., NM, 10,000′ (3020 m), leg. R. Holland.

Fig. 2. *Harkenclenus titus* normal ♂. Same data as Fig. 1.

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# A Study of Isolating Mechanisms among Neotropical Butterflies of the Subfamily Riodininae

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**Abstract.** This paper examines the perching behavior of ten genera of Neotropical riodinine butterflies to determine the nature of perching as a premating isolating mechanism in the context of the tropical forest habitat. The study shows that congeneric sympatric riodinines achieve habitat isolation through mating in different topographic sites and at different times, in addition to displays and pheromones. The study concludes that: 1) perching periods are generally of shorter duration than those of nearctic lycaenids; 2) females actively search out perching sites where they wait for males, when the latter are scarce; 3) spacing of perching sites varies considerably from one genus to the next, as do perching positions; 4) many genera, such as *Nymphidium* have retractable scent hairs, suggesting that pheromones are important as an ethological barrier; and 5) observations of habitat spacing have considerable taxonomic value.

## Introduction

The purpose of this paper is to examine the perching behavior of congeneric riodinine butterflies to determine the nature of perching as a premating isolating mechanism, and the adaptation of this mechanism to the neotropical forest habitat.

Most of the studies of butterfly mating behavior to date have dealt with Nearctic species or with the larger Neotropical butterflies, such as heliconids or nymphalids, whose behavior is more likely to be patrolling than that of perching. The mating behavior of smaller sized butterflies, such as riodinines have been treated in a general way only by Ebert (1967) and Callaghan (1977, 1978). Additional information on this group is spotty at best. Shields (1967), for example, quotes Keith Brown to the effect that many riodinine species hilltop near Rio de Janeiro. No studies to date have examined Neotropical riodinine perching behavior as a premating isolating mechanism.

The following discussion treats the methods used in the study, followed by a description of the different types of riodinine perching localities, the perching habits of ten genera of riodinines, and concludes with a discussion of the nature of riodinid premating isolating mechanisms.

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## Methods

The present study is based on five years of observations of riodinine behavior in many localities, from Southern Brazil to Colombia and Panama. Ten genera and 36 species are treated in the present study. These genera were chosen among many observed because of the relatively large number of observations in each case, and/or because of the greater number of congenerics flying in the same area, and finally, because they were representative of variation in riodinine perching behavior generally. An overall survey of mate locating strategies among riodinines will be included in a forthcoming paper.

I recorded the times, location, and perching position of each observation in the field on a portable tape recorder. On numerous occasions I captured the perching butterfly to make a positive identification. At other times, when I became better able to recognize the perching species from a distance, I would not capture the insect, but note the time and place as usual. If later I returned to the same spot and observed the same or another individual of the same species, I recorded it as a second observation. The times given in the paper are on a 24 hour basis.

As I observed few cases of copulating riodinids, I had to develop a method of distinguishing perching from resting butterflies. Perching behavior is defined as "males resting at characteristic sites and investigating passing objects by flying out at them in search of females" (Scott, 1975). Thus, perching butterflies are always associated with a particular time and place. The problem was to determine the time and place of the perching activity. This I solved by making multiple observations for each species. Species were not included in the study for which the data were too few and/or too widely spread in space and time. Secondly, perching male riodinids often displayed an aggressive attitude towards their own species and towards other butterflies passing by. If they were disturbed, they would eventually return to the same spot. This behaviour is very distinct and hard to confuse with riodinids merely moving through an area.

## Study Area Description

For the purpose of grouping the field observations, I divided the riodinid perching sites into two major categories, and eight sub categories. The two principal ones were forests and hilltops. Forests were subdivided into "outside woods edge", "on woods edge", "treefalls", "inside woods edge", and "sunflecks", designated by the leters "A, B, C, D, and E", respectively. Hilltops were divided into three categories: "hilltop sunflecks", hilltop treefalls", and "open hilltops", referred to as "F, G, and H", respectively. A detailed description of each of these perching sites is as follows:

*FORESTS.*—The great majority of the riodinids are forest butterflies inhabiting the Amazon and Orinoco drainages. As most of the land area is relatively flat and forested, the riodinid forest butterflies have compensated for the lack of prominant topographical features by substituting microhabitats within the forest itself based on sunlight/shadow and the time of day. I have designated five of these, as illustrated in figure 1 and discussed below, in order of decreasing solar exposure.

*A. Outside Woods Edge.*—The tropical forest is far from being a homogeneous mass. It is frequently cut by rivers, streams, campos, and cerrados which delineate definite "woods edge" situations, where the forest stops and another medium begins. Forest species will sometimes be found perching here up to 30-40 meters from the forest margin, usually in the early morning when the first rays of the sun strike the area, to about 800 hours, when the day starts to get hot, and again in the late afternoon, from about 1600 hours to sunset. Males perch on small bushes or other prominent foliage and chase each other vigorously around the area.

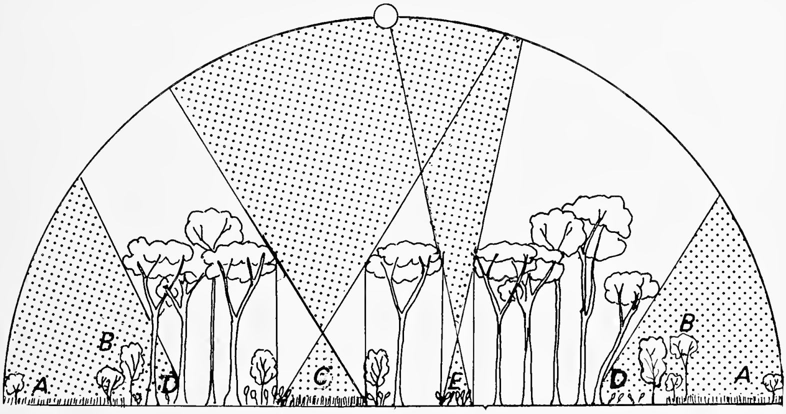


Fig. 1. FOREST PERCHING LOCALITIES
The different forest perching localities described in the text are illustrated in the schematic drawing above. The sun moves in an arc from right to left, illuminating the different localities, shown by the letters A, B, C, D and E.

*B. On Woods Edge.*—In this perching site, the butterflies rest on the outer edge of the forest, usually on or under leaves which shine in the sunlight.

*C. Treefalls.*—Inside the forest, there are significant openings in the canopy through which enough sunlight penetrates to stimulate the growth of plants usually associated with more open areas, such as *Solanum* and various grasses. Young trees from three to four meters high sometimes crowd these areas. This habitat may be caused by a treefall, a logging road, or a small creek. The maximum size of these areas is a height-width ratio of 3:2 at right angles to the path of the sun, as illustrated in figure 1. Areas with a height to width ratio greater than this fall into categories A and B above.

*D. Inside Woods Edge.*—The rays of the late morning or afternoon sun often penetrate the forest edge to strike areas up to six meters inside the forest, "spotlighting" certain foliage, which mark the riodinid perching sites.

*E. Sunflecks.*—Small breaks in the forest canopy allow the sun to penetrate to the forest floor for a few minutes each day, creating a small patch of light, or "sunfleck". This small amount of direct sunlight encourages the growth of broad leafed shade plants, such as *Heliconia* and various *Philodendron* which, when the light strikes them, contrast sharply with the normally barren aspect of the forest floor. These leaves serve as preferred perching localities for many species of forest riodinids, especially during the early afternoon hours. The height to width ratio for this site is at least 5:1.

*HILLTOPS.*—To the north, west, and south of the Amazon-Orinoco drainage, the topography becomes more accentuated and hilltops more prominent as sites for mate locating. Hilltops are defined as accentuated topographic features from which the ground drops away on all sides. They may be located on ridges, but the rule still holds, just that on one or two sides the ground does not drop away as fast as on the others. I define three different hilltop situations, which are illustrated in figure 2.

*F. Hilltop Sunflecks.*—Small breaks in the canopy of a forested hilltop

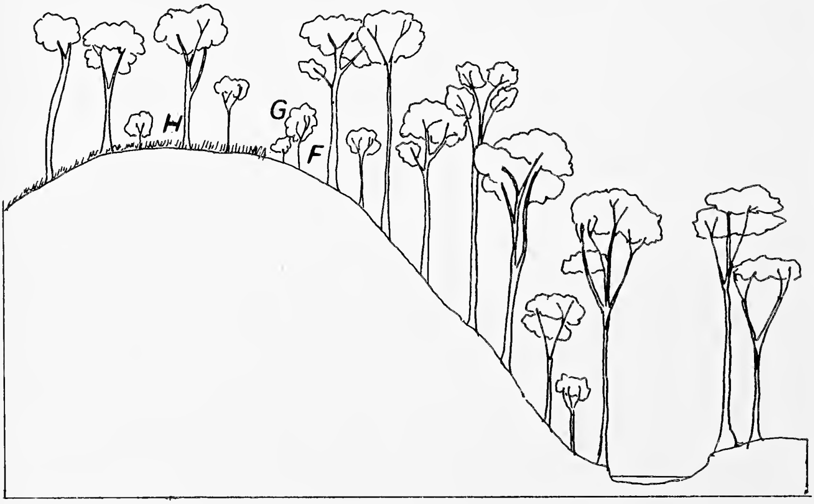


Fig. 2. HILLTOP PERCHING LOCALITIES
In the schematic drawing above, the hilltop perching localities H, G, and F described in the text are illustrated.

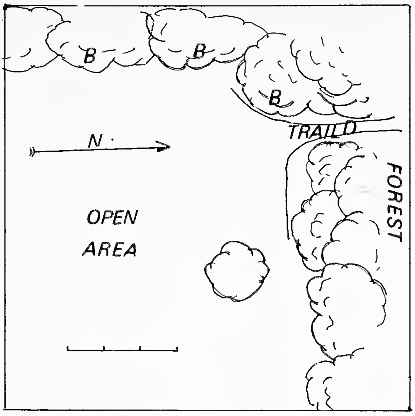


Fig. 3. PERCHING CORNER
The letters refer to sites where perching riodinids await mates during the morning hours. The scale is in meters.

create perching sites where the sun strikes prominent leaves near the forest floor.

*G. Hilltop Treefalls.*—This category is basically the same as "D" above, except that it occurs on hilltops. Openings in the canopy can be caused by wind felled trees, or human intervention.

*H. Open Hilltops.*—These are found in open forest or savanna formations. The ground cover is composed of grasses, small bushes, and/or with a few widely spaced trees. Most of the hilltops in the Brazilian cerrado are this type.

At times, categories G and F may not correspond to the topographically highest spot on a hill, especially if there has been considerable alteration of the hilltop forest.

Finally, the question arises as to where the riodinids perch within the more open localities discussed above, namely sites B, C and D. In my experience, perching usually takes place in what I call "perching corners", illustrated in figure 3. These consist of an opening in the forest, usually in the shape of a corner, or funnel, when viewed from above. Perching butterflies await at the end of the funnel for members of the opposite sex. This behaviour suggests that in forest localities B, C and D mate seeking butterflies of either sex are attracted by lighter areas along the forest edge, along which they move until they become "trapped" in the corner where mates can be found waiting. Figure 3 shows the locations of midmorning perching riodinids in a perching corner, on the side on which the morning sun was striking. The north, or shaded side was without perching activity. Perching corners may be in bold relief, such as the one depicted, or merely a bush which protrudes slightly further from the edge of the forest. However, the existence of a corner appears to be relevant in all cases.

## Results

The perching data for each of the ten genera was placed on graphs, figures 4 through 8, with the hours of the day on the horizontal axis, and the eight perching localities on the vertical axis in accordance with the solar exposure. Midday is shown by a vertical line. The range of the observations for each species is shown by a horizontal line, starting with the hour of the first observation and ending with the last. The total number of observations for each species is also shown on the graph. The hilltopping localities were also included, as I found that in several cases congeneric species were not relegated to only forest or hilltop, but both.

### Genus *Euselasia* Figure 4

Five species fly together in the Xerem reserve near Rio de Janeiro, Brazil. That I found *E. hygenius* (Stoll) and *E. thucydides* (Fabricius) perching in the same site might suggest that spacing was imperfect for the *Euselasia*. However, the phenotypes of *hygenius* and *thucydides* are morphologically quite different. Phenotypically, *thucydides* is similar to *E. utica* (Hewitson), and *E. crinon* Stichel is close to *E. hygenius*. It is these two pairs of species which show the greatest spacing in the habitat.

When perching, the *Euselasia* rest on the underside of leaves with their wings folded over their backs. I have encountered female *Euselasia* rarely, but have on occasion found them frequenting male perching sites at the same time of day.

### Genus *Alesa* Figure 4

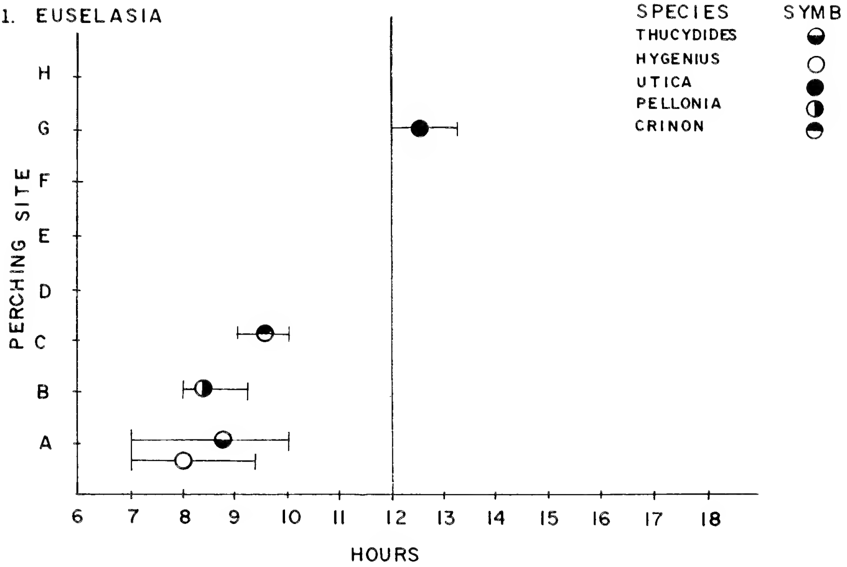
At Villavicencio, Meta, Colombia, two species of the genus *Alesa* may be found hilltopping. I have always observed *A. prema* (Godart) perching on hilltops from central Brazil to Colombia. *Alesa amesis* (Cramer) flies throughout the Amazon drainage and perches in type C and E localities in the forest. Villavicencio is the only locality where I have found *amesis* perching on hilltops. Both species rest with their wings outspread on the upper surfaces of leaves on the hilltop, although *amesis* also rests on the undersides of leaves when perching in the forest. Certain colors and wing patterns may be significant in attracting females of these two species. *Alesa prema* males perch in sunny localities which emphasize the brilliant green upper surfaces of the wings, while *A. amesis* males perch in shaded areas which form a marked contrast with the brilliant white tips of their antennae. Both species demonstrate significant spacing of perching sites and times.

### Genus *Ancyluris* Figure 5

Five species of this genus fly in the Villavicencio area in Meta, Colombia. All five male phenotypes are very similar in appearance, the upperwing surfaces having a red band running from the costa of the forewing to the

FIGURE 4

1. EUSELASIA



2. ALESA

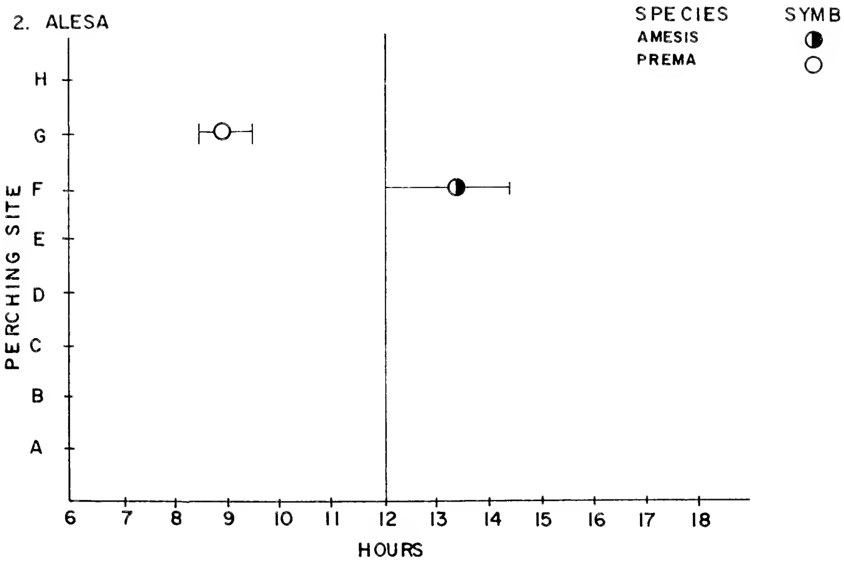
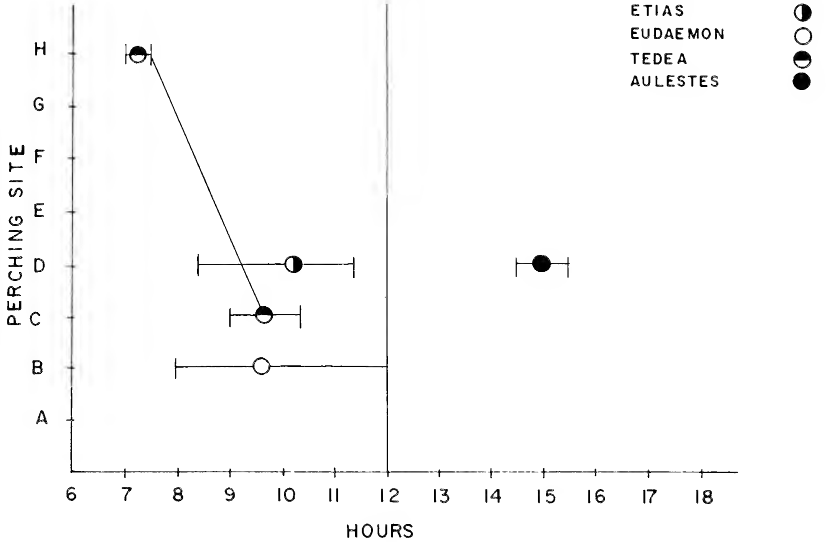
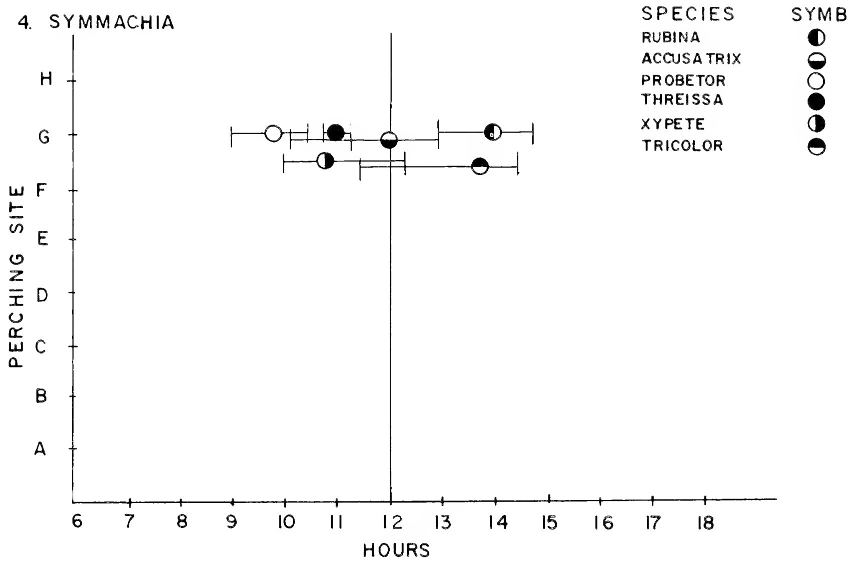


FIGURE 5

3. ANCYLURIS



4. SYMMACHIA



anal angle of the hindwing, and the undersides of the wings displaying a brilliant metallic blue color. However, the female phenotypes of these species are quite different. All these species show significant spacing within the habitat. One, *A. tedea* (Cramer) perches on open hilltops at daybreak then inside the woods edge later in the day. Perching height differs somewhat between species. *A. eudaemon* Stichel perches three to five meters off the ground. *A. aulestes jocularis* Stichel and *A. tedea* rest at heights from one to two meters, *A. etias* (Saunders) less than one meter, and sometimes on the ground. All the species normally perch on the upper surfaces of the leaves with wings flat. Although I have rarely encountered females, I have observed them frequenting male perching sites at the same time of day as the males, which provides an excellent clue as to which females belong to which males.

### Genus *Symmachia* Figure 5

I observed six species currently placed in the genus *Symmachia* hilltopping at Gamboa, Panama. All perch in a type G locality, and various species may fly at the same time. Thus, it would seem that here the breakdown of spacing in the habitat would be complete. However, if the four typical *Symmachia* having the strongly arched costa of the forewing are separated from *S. asclepia xypete* (Hewitson) and *S. tricolor* Hewitson, which do not, the spacing once more becomes apparent. The foregoing suggests that the current taxonomic status of the genus *Symmachia* may not in fact reflect the biological status of these butterflies.

The members of this genus are very fond of hilltops, and rest while perching on the undersides of leaves with their wings outspread.

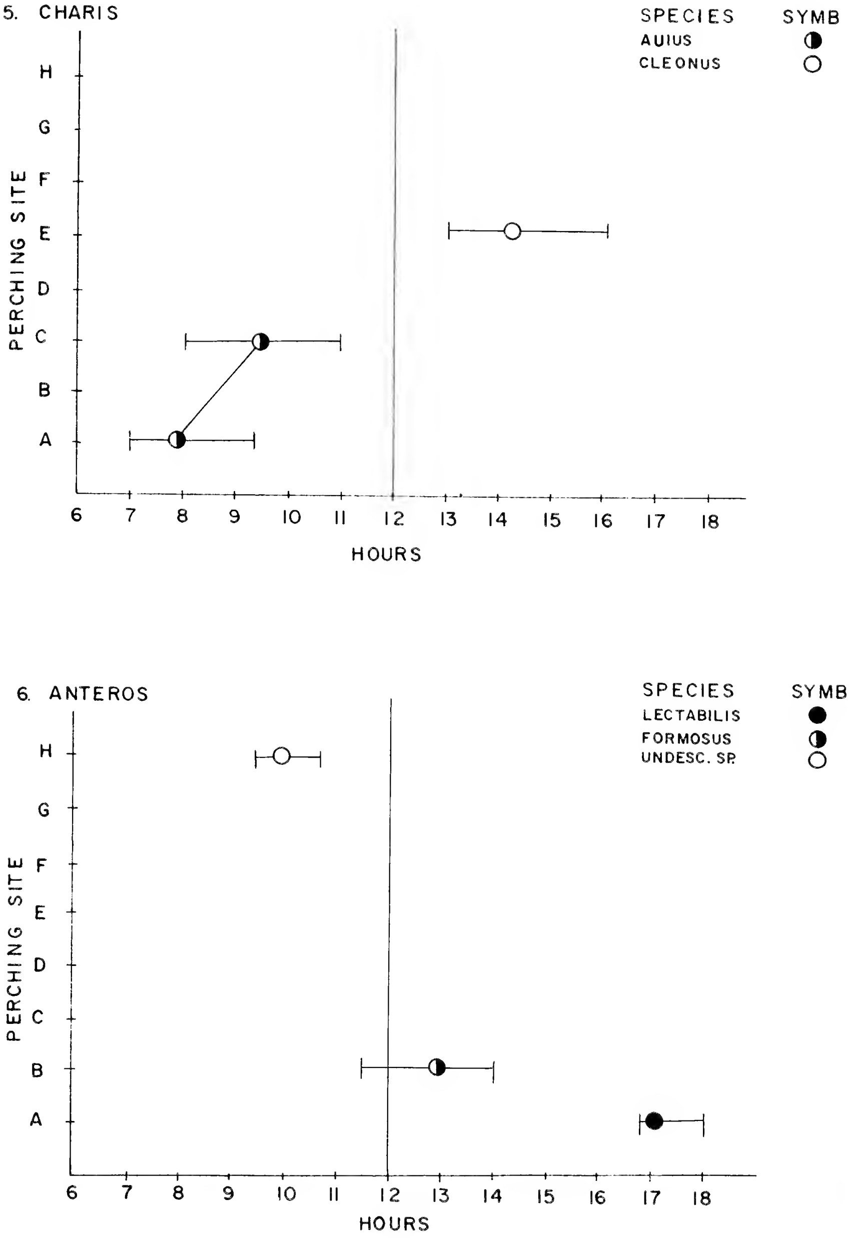
### Genus *Charis* Figure 6

Two species of *Charis* fly sympatrically beside the Rio Negro in Meta, Colombia. I have observed *C. auius* (Cramer) perching in the early morning in type A localities. Later, this species is encountered in D sites. *C. cleonus* (Cramer) males perch in E localities during the afternoon, usually up to three in number, chasing each other around in a tight circle in the sunfleck. Both species rest while perching on the upper surface of a leaf with their wings outspread. I have observed females of both species frequenting the male perching sites, but in smaller numbers and only at times when the males appear to be rarer.

### Genus *Anteros* Figure 6

I recorded the perching habits of three sympatric species of *Anteros* near Felixlandia, Minas Gerais, on the Brazilian Planalto. An undescribed subspecies of *A. carausius* Westwood hilltops during the midmorning. *Anteros formosus* (Cramer) is always found in the early afternoon on or just inside the edge of the gallery woods, and *A. lectabilis* Stichel perches in the late afternoon in the more open cerrado and campos. All three species rest

FIGURE 6


5. CHARIS
SPECIES
SYMB
AUIUS
◑
CLEONUS
○
PERCHING SITE
H
G
F
E
D
C
B
A
6
7
8
9
10
11
12
13
14
15
16
17
18
HOURS
6. ANTEROS
SPECIES
SYMB
LECTABILIS
●
FORMOSUS
◑
UNDESC. SP.
○
PERCHING SITE
H
G
F
E
D
C
B
A
6
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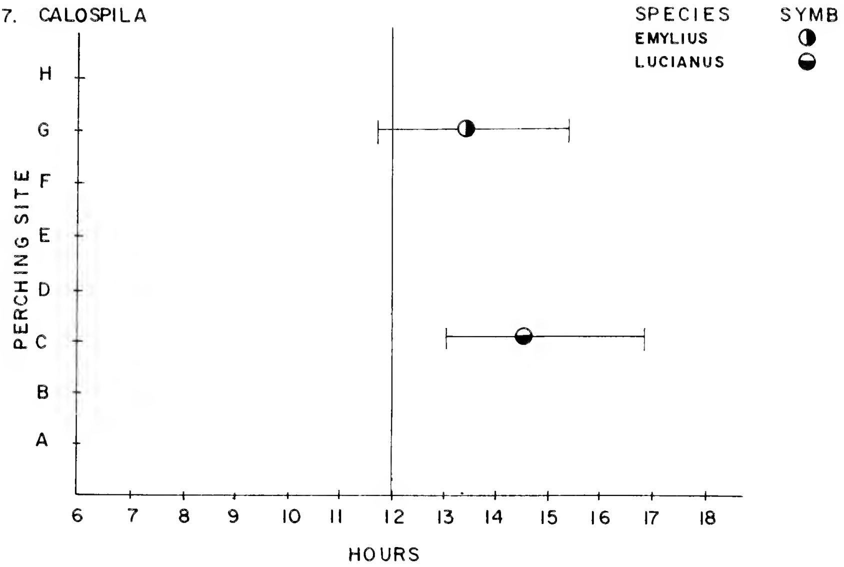
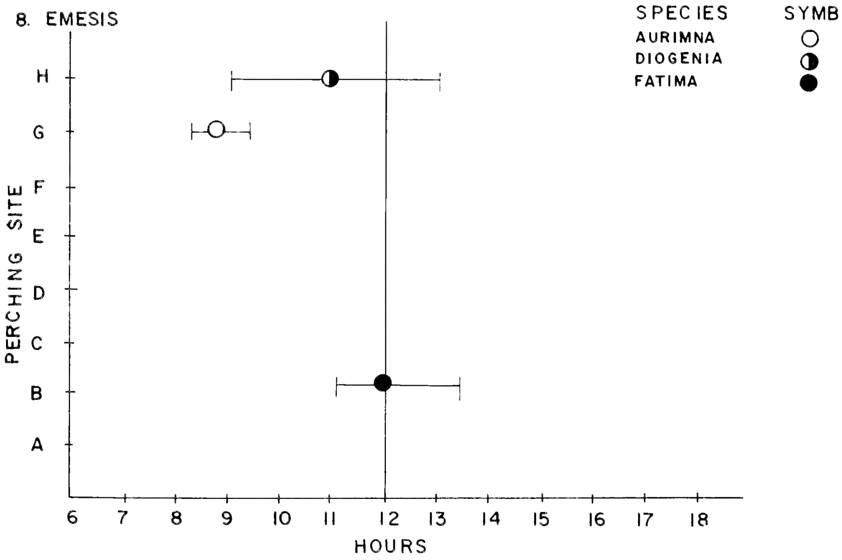
18
HOURS

FIGURE 7

7. CALOSPILA



8. EMESIS



on the undersides of leaves with their wings folded over their backs. To date I have only observed the males perching. The females appear to be much rarer.

Genus *Calospila* Figure 7

Two closely related species of the genus *Calospila* fly near Villavicencio, Meta, Colombia. I found *C. emylius* (Cramer) males on hilltops in numbers of up to 12 individuals during the afternoon. On other occasions, when the males were less common, I found females frequenting the same sites at the same times. *C. luciana* (Fabricius) also perches during the afternoon, but always in woods edge localities. Both species rest under leaves with their wings outspread.

Genus *Emesis* Figure 7

At Villavicencio, I observed three species of the genus *Emesis* perching, all of which demonstrate spacing in the habitat. All these species rest on the upper leaf surfaces with their wings flat, and from one to three meters off the ground.

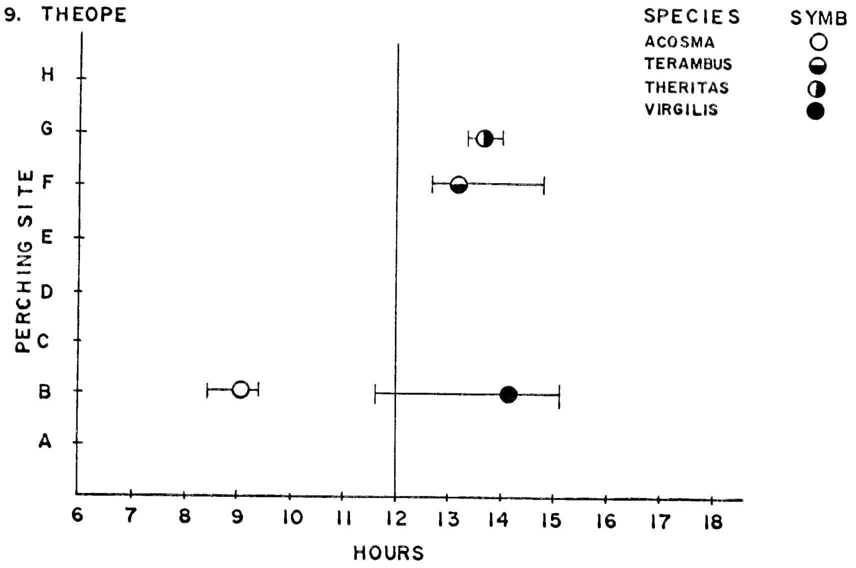
Genus *Theope* Figure 8

Four species of the genus *Theope* are sympatric near Villavicencio. I have found *T. theritas* Hewitson and *T. terambus* (Godart) perching in very similar localities, but never together. After repeated observations I concluded that *T. theritas* perches in slightly more open areas than *terambus*. All the species of this genus rest on the undersides of leaves with their wings over their backs.

Genus *Nymphidium* Figure 8

Four species of the genus *Nymphidium* are sympatric in the Villavicencio area. Three of them, *N. cachrus* (Fabricius), *N. lisimon* (Stoll), and *N. eutrapela (?)* Bates may on occasion be found perching together in type B and C localities. There is no doubt that these three butterflies are valid species, as there are distinct genetalic and other morphological differences between them. This would appear contrary to the contention that congeneric species space themsleves throughout the habitat. However, dissection of the male genitalia of these butterflies reveals scent hairs on the last abdominal segment (Fig. 9). Through observing live specimens, I have discovered that these scent hairs can be extended and retracted much like the hair pencils of certain Danainae. The existence of these organs suggests that pheromones may be important among the *Nymphidium* as a barrier to interspecific mating. Similar organs are found on other closely related genera, such as *Synargis, Juditha,* and *Audre*. What most of these butterflies have in common is that they inhabit open forest formations and savanna which lack the variety of light/shadow combinations found in the forest. The use of pheromones may compensate for this

FIGURE 8


9. THEOPE
SPECIES
SYMB
ACOSMA ○
TERAMBUS ⊖
THERITAS ◑
VIRGILIS ●
PERCHING SITE
H
G
F
E
D
C
B
A
6
7
8
9
10
11
12
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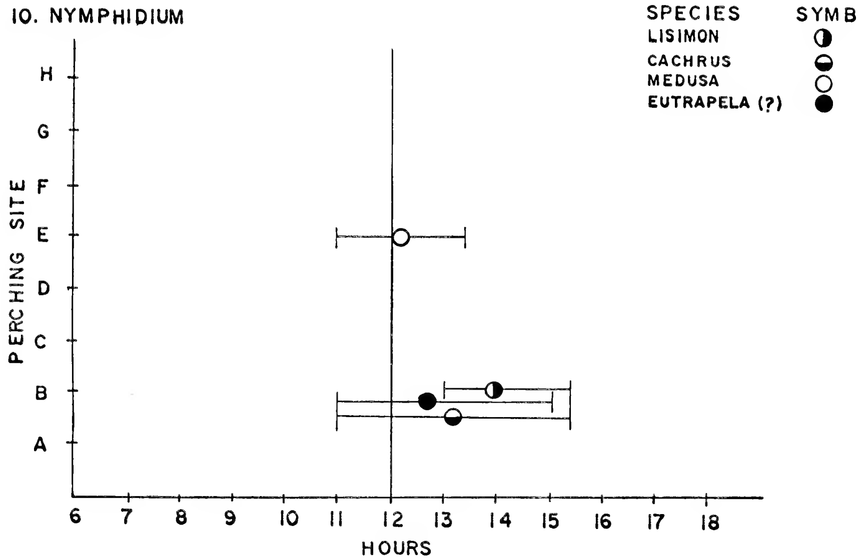
14
15
16
17
18
HOURS


10. NYMPHIDIUM
SPECIES
SYMB
LISIMON ◑
CACHRUS ⊖
MEDUSA ○
EUTRAPELA (?) ●
PERCHING SITE
H
G
F
E
D
C
B
A
6
7
8
9
10
11
12
13
14
15
16
17
18
HOURS

lack of habitat variety among these genera. These structures are also found in the genus *Stalachtis* which inhabit deep woods, are mimetic, and slow flying (Keith Brown, pers. comm.).

## Discussion and Conclusions

The biological properties which prevent the interbreeding of closely related species have been called "isolating mechanisms" since 1937 when Dobzhansky first used the term. These mechanisms were defined by Mayr (1963) as "biological properties of individuals which prevent the interbreeding of populations which are actually or potentially sympatric." Mayr went on to divide isolating mechanisms into two categories; premating, which prevent interspecific crosses and postmating, which reduce their success. He subdivided premating into three parts: a) potential mates do not meet due to seasonal or habitat isolation, b) potential mates meet, but do not mate due to behavioural (ethological) isolation, and c) copulation is attempted but no transfer of sperm takes place due to mechanical differences. Mayr went on to state that habitat isolation is unimportant in mobile animals, and that seasonal isolation is poorly known. In his opinion, the most important mechanisms were behavioural (ethological).

Studies of the mating behaviour of butterflies published since then have

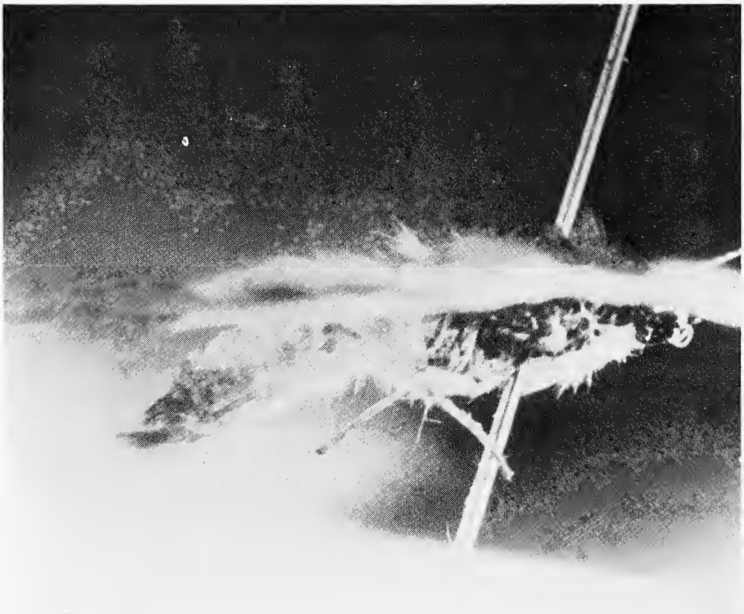


Fig. 9. Dried specimen of male *Nymphidium cachrus* with abdominal scent hairs extended.

shown that partial habitat isolation has been accomplished through mating in different topographic sites within the habitat and at different times. Scott (1975) recorded 18 congeneric pairs of sympatric nearctic butterflies mating in different sites, which included ridges, hilltops, and gullies. Shields (1967) and Scott (1968) examined hilltops as mating sites for many species of butterflies. That many species mate during restricted times of the day has long been recognized by many workers (Miller & Clench, 1968; Scott, 1975; Shields & Emmel, 1973).

The data presented in this study regarding the perching habits of congeneric sympatric species of riodinid butterflies suggest that riodinids have developed a series of complex premating mechanisms in order to maintain specific isolation within the habitat. These mechanisms appear to be in two stages. In the first, similar phenotypes of sympatric species divide the forest habitat into rendezvous sites, defined by different topographic physical features; by light/shadow contrast, and by different hours of the day. The second stage consists of a number of varied ethological barriers, such as displays, and/or pheromones. If for some reason the space/time mechanism fails, then the second stage of ethological mechanisms comes into play.

Scott (1968) and Shields (1967) confirmed that perching and hilltop species are those which have low density populations, and which feed on low density foodplants. These observations characterize most neotropical forest butterflies (Ebert, 1967), and particularly riodinids (Callaghan, 1977, 1978). Scott and Shields also postulated that through the use of rendezvous localities, rarer species could more easily find mates, and through perching for relatively short periods, could keep exposure to predation to a minimum. My observations on riodinid perching habits support this assertion. The fact that riodinid perching was observed at specific times and places attests to the adaptive significance of perching. Through the spacing of perching times and sites throughout the habitat these butterflies save much time, exposure, and effort in avoiding interactions and attempted matings with closely related species.

The data presented in this study suggest a number of conclusions regarding riodinine perching.

**I.** Riodinines perch for relatively short periods during the day. The average perching periods of each genus are shown in the following table:

| **Genus** | **Average Duration of Perching (tenths of hours)** |
|---|---|
| *Euselasia* | 1.9 |
| *Alesa* | 1.3 |
| *Ancyluris* | 2.9 |
| *Symmachia* | 2.8 |

| Genus | Average Duration of Perching (tenths of hours) |
|---|---|
| *Charis* | 2.8 |
| *Anteros* | 1.3 |
| *Calospila* | 3.3 |
| *Emesis* | 2.4 |
| *Theope* | 1.8 |
| *Nymphidium* | 3.4 |
| **Average of 10 genera** | 2.4 |

The above perching periods are short compared to Nearctic lycaenidae, most of which perch "all day" (Scott, 1975). Notable exceptions in Scott's study are *Apodemia nais* and *Apodemia mormo* which perch from 1130 to 1430 and 1100 to 1430 hours, respectively. On the other hand, the average lifespan of Neotropical riodinines appears to be longer (Callaghan, 1978), which suggestss that on the balance, time devoted to mate location over the lifetime of both Nearctic and Neotropical Lycaenids may be similar.

The average perching duration observed of 2.4 hours per day is probably close to the actual average. While some riodinines perch in different habitats at different times, such as *Ancyluris tedea* and *Charis auius*, this seems to be the exception, for continuous observation of all micro habitats in the study areas failed to reveal similar activity by other species. Although I have always made it a point to search the forest canopy, I have never discovered riodinine activity there. The perching duration of hilltopping species is easily measured, as is that of species which perch in open areas. The perching duration of species that perch in D and E areas are harder to determine due to the tendancy of these species to move to other sunflecks once the first disappear into shadows. However, in the present study, only four out of 36 species frequented D and E areas.

**II.** Females will be found frequenting male perching sites. They were never observed to perch in the male fashion, aggressively investigating passing butterflies, nor interacting with each other. In fact, the only way to tell whether the females were actually perching was that the males of the same species had been observed perching at the same time and place. The females were observed rarely, and usually on occasions when the males were scarce. These observations suggest that females actively search out rendezvous sites for mating, and do not just "happen by". This behaviour would eliminate the need for elaborate female rejection rituals, as found in some pierids and heliconids, because females enter the rendezvous areas when they are receptive to mating, and do not when they are not, saving time, energy, and exposure for both sexes.

**III.** The relative spacing between rendezvous sites varies considerably between congeneric sympatric species. Some genera show extremely wide spacing, such as *Euselasia*. Others, such as *Ancyluris* and *Charis* may have species which perch at different sites at different times. At the other extreme, some *Theope* species perch in sites with slight differences and different *Nymphidium* species frequent similar, and sometimes the same sites. In the case of *Nymphidium* other ethological factors, such as chemical signals, seem to be of greater importance.

**IV.** Perching position shows considerable variation between genera. Displays by males are apparently important in *Alesa, Emesis, Charis*, and to a lesser extent in *Nymphidium*, due to the tendancy of these groups to perch on the upper leaf surfaces with wings outspread. The remaining genera hide under leaves at the perching sites. *Euselasia* and *Theope* have cryptically marked and colored undersides of the wings, with eyespots and/or leaf markings. Relative perching height may be an important factor for some genera, such as *Ancyluris*, but the data gathered for the other genera in this respect are inconclusive.

**V.** The prominance of scent hairs in the *Nymphidium* and related groups suggest that pheromones probably play an important role as an ethological barrier to interspecific mating. The majority of the *Nymphidium, Synargis*, and *Juditha* perch for long periods in the same type of open habitat. Encounters between congeneric species must be common. I suggest that genera which perch in habitats which do not afford the variety of light/shadow and topographic site combinations depend more upon ethologcal mechanisms for species recognition than do strictly forest dwelling groups. A third strategy found among savanna dwelling groups such as *Audre, Calephelis*, and *Apodemia*, is that of forming colonies about their foodplant. This strategy will be examined in detail in a forthcoming paper (Callaghan, in prep.).

**VI.** Observations of the spacing of butterflies in a habitat can be of considerable taxonomic value. The genitalia of many closely related riodinid phenotypes are practically identical, as are other morphological characters. Observations on spacing provide many clues not only as to the systematic relationships between questionable phenotypes, as illustrated in the case of *Symmachia*, but as to the sexing of dimorphic species, such as *Ancyluris*. In my opinion, no systematic survey of any group is complete without field observations of habitat spacing.

*Acknowledgments:* I wish to thank Dr. Woodruff Benson of the University of Campinas for his orientation during the development of the project, Drs. Keith Brown, James Scott, and two anonymous reviewers for their helpful comments on the final draft. Finally, my thanks to Dr. Robert Robbins for his perching records on Panamanian riodinids.

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# Mate-Locating Behavior of Western North American Butterflies. II. New Observations and Morphological Adaptations

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**Abstract.** New observations on mate-locating behavior of various western United States butterflies and skippers are given. Some species show a certain amount of flexibility in behavior, especially at high density when several normally hilltopping species search for mates around dense stands of the larval foodplant. Several data sets were examined that indicate the rarity of hilltopping species compared to other species, that seem to reaffirm the usefulness of hilltopping at low density. Perching species, when compared with closely related patrolling species, have more pointed forewings and more powerful thoraxes compared to the size of the wings; perching species commonly have faster wingbeat frequency, and often have the forewing veins more crowded toward the costa. These adaptations presumably give perching species a powerful takeoff from rest for the approach and maneuver to a passing female. Females do not need this takeoff and tend to have more patroller-type wings.

## Introduction

Scott (1975) reported the methods that males use to find females in many western North American butterflies and skippers. This paper gives additional information, including species not previously studied, and much more extensive observations on some species previously studied.

A few definitions are worth repeating. In *perching behavior*, males rest at characteristic sites and investigate passing objects by flying out at them to search for females; females fly to these sites to mate, then depart. In *patrolling behavior*, males fly almost continuously in search of females. In the third paragraph of page 2 of Scott (1975), the sentence "In patrolling species, interactions occurred predominantly when resting males investigated moving objects," was created by the printer by combining parts of the two adjacent sentences. It is wrong and should be crossed out. Perching males investigate females by flying from a resting position, whereas patrolling males investigate females by spotting and pursuing them while flying.

Methods are those of Scott (1975). Twenty-four-hour Standard Time (not Daylight Saving Time) is used. All observations were done in the foothills of the Front Range in Jefferson County, Colorado, unless otherwise stated.

## New Observations on Mate-Locating Behavior

*Papilio eurymedon* (Lucas). In 1980 adults of *eurymedon* and *P. glaucus rutulus* were unusually common in the Front Range foothills. Male *eurymedon* were found to choose open lanes among trees on hilltops and ridgetops, where they patrol back and forth in the little forest glades. Males seldom rest; they patrol most of the time. Males are usually found on hilltops, but they sometimes feed on mud or flowers in valley bottoms. One male was observed chasing a *rutulus* in a gulch at a patch of *Apocynum* flowers.

*Papilio glaucus rutulus* (Lucas). Male *rutulus* were also encountered frequently patrolling in little forest glades on hilltops and ridgetops. However, whereas *eurymedon* males stayed a long time and returned repeatedly to a given spot, *rutulus* males stayed only briefly before departing, presumably to other wooded slopes and valley bottoms. *P. multicaudata* (Kirby) patrols in gulch or valley bottoms only (Scott, 1975), so *rutulus* seems to have a generalist strategy, while the other two species are specialized.

*Papilio zelicaon* form *nitra* Edw. Considerable effort was made to study *nitra* in 1980, when adults were the most common I have ever found them in the foothills of the Front Range Colorado. Males patrol and perch on hilltops as reported by Scott (1975). Fisher (1977) showed that *nitra* is a form of *zelicaon* Lucas. A 1981 cross of a typical male *nitra* X female *zelicaon* from Jefferson County Colorado supports this conclusion, as typical *nitra* and *zelicaon* offspring resulted. Male behavior of *nitra* and the sympatric form *zelicaon* and *P. polyxenes* Fab. were observed for differences. One phenomenon became apparent: *nitra* males seem to occur nearly always on the topmost point of a series of hills. In 42 observations in 1979-1981, *nitra* males were found on the topmost hill at a locality, and in only 13 cases was *nitra* found on a lower adjacent hill. In contrast, form *zelicaon* when common is distributed rather continuously from the top points of the ends of the ridges, along the ridges sloping up to the high points, and on top of the hills as well. *P. polyxenes* males often occur on the highest point also, but they are also often found perching on a shelf-like slope just below the hilltop itself. These behaviors of *zelicaon* and *polyxenes* are understandable because they distribute the males along the ridge system where females come to mate. But *nitra* is rare—seldom more than one male found at a locality and usually none—and it does seem to be found on the topmost points more often than would be expected if it interacted with other individuals like an ordinary male *zelicaon*. At one locality 48 different male *zelicaon* were found, all over the ridge system, but the three male *nitra* found were only on the topmost two adjacent points of the mountain. Perhaps form *nitra* gains an advantage in mating if the topmost point receives more females. Form *nitra* appears only in hilly areas in its range, which is consistent with the hypothesis. There are perhaps survival differences between *zelicaon* and *nitra* also that prevent *nitra* from occurring at higher altitude than the Transition Zone foothills (form *zelicaon* extends to the Canadian Zone and sometimes higher). Hybridization with *polyxenes* seems to occur frequently also (intermediates between *nitra* and *polyxenes* of every possible combination fly along with *nitra, zelicaon* and *polyxenes*), and hybridization probably first introduced the black genes into the *zelicaon* gene pool. Because *polyxenes* is a lower altitude insect than *zelicaon* in general, the influx of *polyxenes* genes into *zelicaon* that probably created *nitra* may have included linked genes giving *nitra* a survival advantage at low altitude.

*Pieris callidice occidentalis* (Reakirt). Males patrol almost constantly, and patrol and chase others on hillsides as well as hilltops, although at low density hilltops are the most reliable places to find them. Localities studied were the foothills of the Jefferson County Front Range; Loveland Pass, Summit County Colorado; various alpine sites in the San Juan Mountains of Hinsdale and Ouray Counties, Colorado; Mt. Sherman, Park County, Colorado.

*Colias pelidne* Bdv. & LeC. Males patrol about ⅓ m above ground all day in valley bottoms or slopes near shrubby willows and *Vaccinium* (Round Lake, Wind River Mountains, Sublette County, Wyoming).

*Colias scudderii scudderii* Reak. Males patrol swiftly all day about shrub willow areas in valley bottoms (So. Rio Grande Reservoir, Hinsdale County, Colorado; Loveland Pass, Summit County, Colorado; Toll Ranch, Gilpin County, Colorado; north of Greenhorn Peak, Pueblo County, Colorado).

*Colias scudderii harroweri* Klots. Males patrol, in morning at least, in bogs with small shrub willows (Canyon Creek, Wind River Mountains, Fremont County, Wyoming).

*Erebia magdalena* Streck. Males patrol all day over rockslides as Scott (1975) states, but extensive observations indicate that males patrol much more often in hollows in the rockslide than on evenly sloping or convex parts of the rockslide, which they cross fairly rapidly (Loveland Pass, Clear Creek County, Colorado, various sites in alpine San Juan Mountains, Colorado).

*Oeneis jutta* (Hubn.). Males perch, and occasionally patrol, in partly shaded small forest clearings (about 3-6 m wide) on fallen lodgepole pine logs and sometimes tree trunks or other objects, mainly in gently sloping swales in grassy forest. They do this at midday at least, in Middle Park, Grand County, Colorado.

*Oeneis chryxus* (Dbldy.). At timberline at several localities in the San Juan Mountains in Hinsdale County, Colorado, male *chryxus* perch in gulch bottoms and investigate passing objects, rather than on hilltops as they do in most areas. The only hilltops there are far above timberline where *chryxus* was not found, so the *chryxus* of this area have evidently adjusted for the lack of nearby hilltops.

*Oeneis melissa* (Fab.). Males usually perch, and sometimes patrol, on rocky hilltops and ridgetops. In 1980, on a very windy day, males were observed perching and chasing in steep rocky chutes on hillsides also. On calmer days males were observed chasing on rockslides on slopes as well as hilltops. *O. melissa* seems restricted to rocky areas, whereas *O. polixenes* (Fab.) and *bore edwardsi* dos Passos males perch and patrol in heavily vegetated swales from the middle to the base of slopes, or swales in flatter hummocky areas, based on extensive 1979-1981 observations (for *melissa*, McClelland Mountain, Clear Creek County, Colorado; Loveland Pass, Clear Creek County, Colorado; Hermit Pass, Custer County, Colorado; Mt. Sherman, Park County, Colorado. For *polixenes*, Loveland Pass, Mt. Lincoln, Park County, Colorado, McClelland Mountain, Mt. Sherman. For *bore*, Cottonwood Pass, Chaffee County, Colorado, and many alpine sites in San Juan Mountains, Colorado).

*Speyeria edwardsii* (Reak.). Males frequently patrol all day in shrubby areas just below hilltops, although they sometimes patrol elsewhere also. Many males were seen to patrol there, often in areas where *Papilio indra* Reak. perches just off the summit, and a copulating pair was found off of a hilltop at one site.

*Boloria improba acrocnema* G. & S. Males patrol slowly all day about 10 cm above ground in moist slopes and swales. Males were observed chasing and courting females, and pursuing *Speyeria mormonia* etc., from 0905 to 1540 (San Juan Mountains, Colorado). Another paper gives the complete life history, and its ecology, and assigns it to *B. improba*.

*Boloria napaea halli* (Hoffm.). Males patrol swiftly all day about ⅓ m above ground, in moist meadows where *Polygonum bistortoides* (Pursh.) Small is common (Wind River Mountains, Sublette County, Wyoming).

*Boloria kriemhild* (Streck.). Males patrol all day about ⅓ m above ground in moist meadows or boggy areas (Wind River Mountains, Sublette County, Wyoming).

*Chlosyne palla* (Bdv.). At a low density population in 1980, males perched on small dirt plateaus in the gulch bottom, as described by Scott (1975) (near Idledale, Jefferson County, Colorado). However, at another site, the same hillside burn where *Erynnis martialis* was common on Ralston Butte, adults and the larval foodplant *Erigeron speciosus* var. *macranthus* (Nutt.) Cronquist were both very common. Males patrolled about a north and northeast facing hillside near the plants, in an area which was partly grassy, partly covered with shrubs, and partly open woodland. Numerous courtships were observed, and egg clusters were found on the foodplant.

*Chlosyne gabbii damoetas* (Skinner). Males both perch and patrol frequently in rocky hollows and chutes, and roads cut across rockslides, all day in the San Juan Mountains, Colorado.

*Poladryas minuta minuta* (Edw.). Observations in 1972 in Baylor County, Texas, and in 1978, 1979, and 1980 in Colfax County, New Mexico, show that the mate-locating system is the same as that of *P. minuta arachne* (Edw.). Males perch on hilltops and ridgetops in the morning (at least from 0730-1130), then depart and are found on flowers elsewhere in the afternoon.

*Nymphalis milberti* Godart. Extensive observations in 1980 show that the main sites of mate location are the slopes and especially rocky places just below a hilltop, usually on the west (sunny) side of the hill. These places are the same perching sites as for *Papilio indra*, and the two species are usually found together. Other sites such as gully banks are chosen rarely (one observation by Scott, 1975, on the Colorado plains in Boulder County), at least where hills are available (the gully bank observations was on the Colorado plains). Males perch from late morning until late afternoon; observations were made at 1050, 1100, 1115, 1130, 1200, 1213, 1215, 1230, 1330, 1340, 1413, 1445, and many others in the afternoon. These observations were all in the spring, as the fall overwintering individuals do not seem to show mate-locating behavior. In *Nymphalis antiopa* (L.) only the spring overwintering adults have been observed chasing and mating also (one mating observed 28 April 1965 in Gregory Canyon, Boulder County, Colorado).

*Apodemia nais* (Edw.). In 1980 the mate-locating repertoire of *nais* was expanded somewhat. Males were observed chasing and investigating others at 0850, 0900, 0915 to 1030, 0930, 1230, 1300-1330, 1412, 1420, and 1430, extending the time span of male mate-locating behavior considerably (Scott, 1975 reported 1130-1430 in a gulch bottom). Males were observed perching in sloping gulches in 1978 and 1979. In 1980 adults were abundant on slopes near their larval foodplant, *Ceanothus fendleri*. Males perch often in hillside swales there, and males often patrol in an erratic flight over the canopy of the blooming *Ceanothus* and between the plants. Perching males fly out at other insects from their perches. Courtship was observed as early as 0900 as a male repeatedly followed a female ovipositing on the *Ceanothus*. Perching males rest on twigs etc. about ¼ m above ground, the height of the prostrate *C. fendleri* plants. Density was high in 1980, which may have increased the areas (and times?) used for mate location.

*Strymon melinus* Hubn. Males normally perch on small trees or shrubs on hilltops in afternoon only (Scott, 1975), but in 1979 three males were observed perching there at 1115, unusually early for the species.

*Callophrys sheridanii* ssp. Near Paradox in Montrose County, Colorado, males of this ssp. (an undescribed spp. basically intermediate between *s. sheridanii* Edw. and *sheridanii comstocki* but with fewer ventral hindwing spots than either) perch on shrubs and other objects about ½ m above ground in the bottom of gulches, at least from 1200-1400, when a few chases were observed; behavior is very similar to a Churchill County, Nevada, *sheridani* population described by Scott (1975).

*Vaga blackbruni* (Tuely). On Oahu, Hawaii, males patrolled and chased others on the canopy (3-7 m high) of prominent trees on a hilltop. They patrolled the sunlit part of the canopy during sunny periods (from 1300-1400 at least) and rested on leaves when clouds obscured the sun.

*Plebejus melissa* Edw. Males patrol like other blues to find females. One male however, was observed perching on a 15 cm tall plant and darting out at passing blues, at 1235 in the foothills of Jefferson County, Colorado, 28 June 1978. Perching behavior is very rare in this species however; the only species of blue (Polyommatini) which I have studied that frequently has perching behavior is *Everes amyntula* (Bdv.) (Scott, 1975).

*Thorybes mexicana* (H.-S.). Males almost always perch on hilltops, based on extensive observations at numerous localities. However, in 1977 at the Moffat Tunnel in Gilpin County, where there are no hilltops for miles (only valley and wooded hillsides), males were observed perching in swales and a courtship was seen at 1235 in a swale. Near Hopewell Lake, Rio Arriba County, New Mexico, where no hilltops were available, a male was observed perching and chasing in a swale, and others perched on a slight prominence on a hillside.

*Thorybes pylades* (Scud.). This species is normally rare in Colorado, and the observations cited for Texas and Colorado by Scott (1975) were nearly all done in west Texas, where males perched in a gulch. In 1980 many males were watched in Jefferson County, Colorado; all perched and investigated over butterflies on or near hilltops, not in gulches, at about 0859, 0911, 0937, 0944, 1141, 1400, 1415, 1500, and 1540. *T. pylades* therefore seems to be a hilltopper in general (they also perch on hilltops in Arizona, Utah and El Dorado and Colusa Counties, California), except in West Texas where hilltops were not studied. The Colorado males observed all perched bertween shrubs or small trees, either on the very top of the hill or within 12 m of the hilltop on the sunny side of the hill, except for one male which perched in a small (⅔ m deep) depression in a hillside. Males rested on twigs,etc. roughly ½ m above ground, between flights investigating other butterflies, flies, etc. Ray Stanford (pers. comm.) observed that males at Aspen, Pitkin County, Colorado, perch among shrubs on hills a short distance from the exact top of the hill where *Thorybes mexicana* and *Erynnis brizo* (Bdv. & LeC.) perch. *T. mexicana* males perch on stones, etc. on the top of a hill, usually in open areas, in contrast to *pylades* which perches among shrubs, often on the top but frequently a short distance from the top. Comparison no. 12 on page 31 of Scott (1975) between *pylades* and *mexicana* is therefore more like the comparison between *Papilio zelicaon* and *P. indra* (which mate on the top of the hill versus just off the top) than like the other comparisons.

*Erynnis pacuvius* (Lintner) and *E. martialis* (Scud.). *Pacuvius* is normally rare in Colorado, seldom more than one seen per day, but at Ralston Butte in Jefferson County, Colorado in 1980, an old east-facing burn was found with a large population of *Ceanothus fendleri* plants, the larval food of both species. Males of both *Erynnis* were common and patrolled rapidly between and over *fendleri* bushes looking for females (often chasing other males). Under normal density conditions (Scott, 1975), males of both species perch on hilltops and are rarely seen elsewhere. *E. pacuvius* males also patrolled near hillside *Ceanothus* at Golden Gate Canyon, Jefferson County, where this plant and adults were very common.

*Erynnis brizo.* Males normally perch on hilltops, but when they are abundant I have also observed many males patrolling among the larval foodplant (*Quercus gambellii*) on hillsides at Jarre Canyon, Douglas County, Colorado. The only copulating pair found there was on the hilltop.

*Polites sonora* (Scudder). Courtship is frequent at flowers (of *Cirsium drummondi* var. *acaulescens* in Colorado) in Colorado as well as in California, in addition to the usual male perching in low spots of meadows (east of Gunnison, Gunnison County, Colorado; Toll Ranch, Gilpin County, Colorado).

*Hesperia leonardus montana* (Skin.). Courtships occur mainly at flowers, all day, and little or no mate-location seems to occur elsewhere. A hilltop 50 m from where *montana* was common attracted *H. pahaska* Leuss. earlier in the summer, but no *montana* when *montana* was common on *Liatris punctata* flowers nearby (near Deckers to town of South Platte, Douglas and Jefferson Counties, Colorado).

*Hesperia uncas* Edw. This species normally perches on small ridges or hills to find females, but in 1980 at a patch of *Cirsium vulgare* thistles I observed a male which had been resting on a thistle flower pursuing a female in a valley bottom. *Hesperia ottoe* Edw. males that were resting on flowers were pursuing passing objects there also, but this is the only mate-locating behavior known for *ottoe*, which seldom occurs away from flowers (Scott, 1975).

## Hilltopping and Rarity Revisited

Scott (1970) found that species that mate on hilltops were only one fourth as common on the average as species mating elsewhere. However, several of the species listed as hilltoppers in Table 3 of that paper were later (Scott, 1975 and this paper) found not to be hilltoppers (*Hesperia juba* (Scudd.), *Erynnis icelus* (Scudd. & Burg.), *E. afranius* (Lintner), *E. telemachus* Burns, *Euchloe ausonia ausonides* Lucas, and *Speyeria coronis* (Behr)) because, although they rarely occur on hilltops, they do not show mate-locating behavior on hilltops. Recalculating the data when these species are transferred to the non-hilltopping category, the mean abundance of hilltoppers is 0.24 specimens per hour, the mean for non-hilltoppers is 0.97 specimens per hour. The difference actually is increased; now the hilltoppers are less than one fourth as common as the non-hilltoppers.

This study (Scott, 1970) only considered spring species (March-May), so it may be worthwhile to consider another data set for the whole season using different methods. Marc Epstein and I have accumulated records for the butterflies and skippers of Red Rocks Park, Jefferson County, Colorado, from 1963 to 1980. Thousands of records were obtained, by 13 collectors; we will publish a paper on their phenology elsewhere. The records for each species were plotted, each brood delineated, and for each brood for which the number of records N is greater than or equal to 5, the standard deviation of flight date was calculated, which is an estimate of the "spread" of the flight period. The abundance of one brood of a species can be calculated as the number of records divided by twice the standard deviation. Dividing by twice the standard deviation compensates for differences in lengths of flight periods, and the resulting records per day abundance is roughly comparable to the specimens per hour of Scott (1970). The average abundance of non-hilltoppers is 0.60 records per day (for 49 broods), the average for hilltoppers is 0.47 (for 24 broods). There is still considerable difference between them (p less than 0.05), despite the fact that the protocol is not favorable for showing such differences (only presence or absence on a given day is recorded rather than the actual number of individuals seen or collected, so slight differences are apt to be obscured). The average number of records per species is also greater for non-hilltoppers (19.6) than for hilltoppers (14.5), although the average standard deviations of flight time are very similar (17.4 versus 16.6 days).

## Morphological Adaptations to Perching Versus Patrolling Behavior

When the wing shape, body size, and flight pattern of perching species are compared with patrolling species, differences are evident.

Perching species in many cases have the forewings more pointed, with the margin straight from about vein $M_2$ to the tornus, whereas patrolling species have the forewing less pointed with the margin fairly evenly convex. Among the Pyrginae, *Thorybes* and *Erynnis* perch and have the former shape, while *Staphylus, Pholisora* and *Celotes* patrol and have the latter shape. Among the hairstreaks, most species perch and have the former shape, but *Hypaurotis crysalus, Habrodais grunus, Satyrium fuliginosum,* and *Phaeostrymon alcestis* all patrol and have the latter shape. Among the *Hesperiinae, Copaeodes aurantiaca* has the former shape and perches, but the tiny patrolling skippers *Ancyloxypha numitor, A. arene, Adopaeoides prittwitzi* and *Piruna pirus* have the latter shape. Some tiny patrolling Hesperiinae (*Oarisma*) have the straight forewing margin, but the ratio of the maximum forewing length to the distance from the wing base to the tornus is still smaller (it is about 1.50 in *Copaeodes*, about 1.26-1.38 in the other Hesperiinae mentioned). This ratio is greater in the satyrs that perch (averaging 1.50 among the nine *Oeneis* and *Neominois* species) than in those that only patrol (averaging 1.34 among 13 species). The ratio is greater among the Colorado *Papilio* that frequently perch (averaging 1.68 among *bairdii, polyxenes, zelicaon,* and *indra*) than among those that nearly always patrol (averaging 1.58 among *multicaudata, eurymedon, glaucus rutulus*).

Perching species tend to have a large muscular thorax in relation to the size of the wings. When species of the same wingspan are compared, the perching species have thicker more muscular thoraxes than patrolling species. The perching species of *Polygonia* and *Vanessa, Asterocampa*, most hairstreaks and coppers, and most skippers (except the patrolling skippers just mentioned) have thick bodies compared to their short wings. Nearly all the butterflies with a muscular thorax are perching species. *Parnassius* seem to be exceptions (although they have rounded forewings); I think the large body of *Parnassius* may simply be very hard to crush. They are distasteful (T. Eisner, pers. comm.) and birds probably let them go after mouthing them.

Perching species also seem to have a greater wing beat frequency, a subjective field impression. Many patrolling species simply flutter past the observer.

A complete analysis of morphological adaptations would be a major study. It would include the body weight, thorax weight, forewing length and shape, and hindwing length and shape, and even the arrangement of the veins in the wings, flight speed and wing beat frequency, analyzed using the principles of aerodynamics. The forewing veins seem to be crowded toward the costa in many perching species. This complete analysis does ot appear to be simple, because the optimal design of the wings appears to change with wing size. The large butterflies (*Danaus, Papilio,Speyeria*) have rather pointed forewings even if they patrol to find females. Tiny insects such as Thrips (Thysanaptera) and some tiny moths literally "swim" through the air because of their high "Reynolds Number" (Pringle, 1957), so their wings can be shaped like oars; this principle may be applicable to tiny butterflies like *Brephidium, Zizula* and *Philotiella*. The aerodynamic aspects of these morphological adaptations have not been adequately studied at the present time. Kammer's (1967) studies of the thorax muscle firing sequence, and Nachtigall's (1965, 1967) studies of lift and drag of dead Lepidoptera adults are a start in the study of Lepidoptera flight, but are only peripherally relevant to the problem, because studies of flying animals are needed.

By analogy with the wing shape of airplanes and birds, the functional utility of the morphological differences can be surmised. When a resting perching male spots a passing creature, he needs power, speed and maneuverability from a muscular thorax and pointed wings for a quick takeoff and approach to the passerby, like a powerful stubby-winged jet plane. A patrolling male, however, needs larger wings (with extensive wing area for extra lift) and a less powerful body for a nearly constant flying search, like a glider plane. These differences are also obvious among birds (compare kestrels, hummingbirds and flycatchers to *Buteo* hawks, vultures and albatrosses, for instance).

Nachtigall (1967) found that the aerodynamic characteristics of all the species studied were similar (plots of lift and drag when the wings were held fixed to the side in wind tunnels), and the major factor increasing the lift/drag ratio was increased speed. This may mean that the ratio of thorax muscle power to wing area may be the important aspect that differs between perching and patrolling butterflies. To increase this ratio, perhaps the rear part of the forewing and the hindwing are less important in flight and so it is these parts that shrink in perching species. This shapes the wings more like a propeller which presumably gives more forward thrust for extra speed. The speed perching males need to overtake females seems to give them additional lift which compensates for the loss of these wing areas. In other insects too, it seems that the faster the wings are flapped, the narrower they become. The rapid wingbeat species like Sphingidae, flies and most wasps have narrow wings and small hindwings, whereas slow wingbeat species such as Saturniidae and grasshoppers have broad wings. Kammer (1967) found that cutting off part of the wings of *Hylephila* did not affect the wingbeat frequency much, so the wingbeat frequency seems to be an evolved aspect of the neural mechanism rather than a direct result of the wing shape.

Females of perching species do not exhibit perching behavior. As one would expect, their wings tend to be more rounded than wings of their males (compare female with male *Hesperia*, etc.).

## Discussion

The explanation of the cause of hilltopping species being rarer given above (that hilltops are mating rendezvous, allowing rare species to survive; at high density mating occurs more widely in the habitat so hilltopping has little value) seems to be supported by the observational data. At high density *E. brizo, E. martialis* and *E. pacuvius* males (plus other species, *C. palla* and *A. nais*, that do not mate on hilltops) were all observed searching for females at dense stands of the larval foodplant, so hilltopping seemed to have little value in high density conditions. High-density species should seldom evolve hilltopping. Furthermore, Scott (1975, pp. 32-33) discussed a mechanism of evolution of separate mating sies among closely related species, in which the rarer species would be more likely to evolve mating in sites such as hilltops.

The observations seem to demonstrate a certain flexibility in mate-locating behavior, of some species at least. Such flexibility is well known in vertebrates. The five species just cited demonstrate a flexible response to density. Shapiro (1970) found that the normal perching behavior of *Euphyes bimacula* Gr. & Rob. changed at high density. Two species (*P. eurymedon* and *P. sonora*) were observed courting at flowers, in addition to the usual places of mate location, and other cases of this are given by Scott (1975). The observations on *O. chryxus* and *T. mexicana*, plus Scott's (1975) observations on *Euphydryas*, indicate a certain amount of local adaptation to the topographic sites available in the habitat. Scott (1975) mentioned species that both perch and patrol. Theoretically, one would expect a butterfly species to evolve a mate-locating strategy or location and time of mating to improve mating success, but a species should retain the capability of mating under other circumstances if the opportunity arises. For instance, if a male of a hilltopping species flies off of a hilltop to find flowers, if a receptive female happens to be at an adjacent flower the species should retain enough flexibility for mating to occur there. After all, the ultimate purpose of special adaptations for mate-locating behavior is to increase mating efficiency. The morphological adaptations probably increase mating efficiency, because the muscular thoraxes of perching males probably enable them to catch up with more females, and the larger wing area of patrolling species probably allows them to fly farther on the same energy input and thus discover more females.

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# Polymorphism in *Satyrium calanus* (Huebner) from Wyoming and Colorado (Lepidoptera: Lycaenidae: Theclinae)[1]

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**Abstract.** Some populations of *Satyrium calanus* in Wyoming and Colorado are polymorphic. These various forms are discussed and illustrated.

## Introduction

In a recent paper, the author discussed some of the forms of *Satyrium calanus* (Huebner) that occur from northern New Mexico to southern Wyoming (Ferris, 1981(82)). The manuscript for this paper was originally submitted for publication in early 1980. In the ensuing period, additonal specimens have been obtained from southern Wyoming and further comments are in order. Two other publications, discussed below, have also treated the insect as it occurs in the Rocky Mountains.

Throughout most of the Rocky Mountain region, *S. calanus* is referable to the subspecies *godarti* (Field), a typical male of which is shown in Figs. 1-2. Phenotypic variation within what is considered normal *godarti* was discussed by Ferris (1981(82)) and by Fisher in Ferris & Brown (1981). The species as a whole uses oak as the larval host, although other plants are occasionally reported. The distribution of *S. calanus* in the Rocky Mountains is thus restricted to regions in which oak occurs, usually *Quercus gambelii* Nutt.

In 1904, James Fletcher described what he thought to be a new species, *Thecla heathii*, from southern Manitoba. Field (1938) first reduced this taxon to the status of an aberrational form, and subsequent authors have concurred with Field's action (Brown, Eff & Rotger, 1957; dos Passos, 1964). Miller & Brown (1981) omitted the taxon entirely. Based upon its collection locality, "heathii" is an aberrational form of *S. calanus falacer* (Godart). Fletcher described "heathii" based upon a single female specimen.

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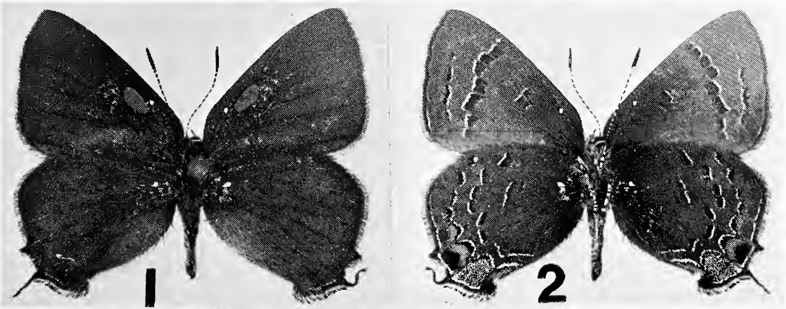
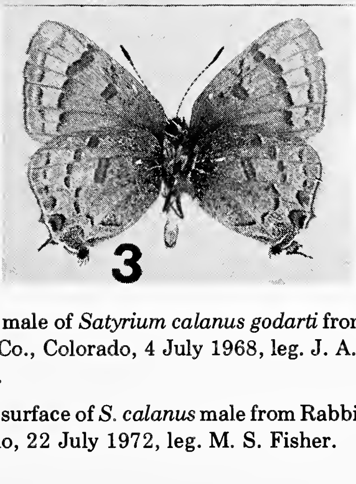
As noted by Fisher (1976), the "heathii" aberration occurs rarely and he listed records from Manitoba, Michigan and Colorado. Muller (1976) figured a specimen from New Jersey. The first Colorado record, a single specimen, was reported by Stallings & Turner (1943) from Beulah, Pueblo Co., on 6 July 1942. A decade later, J. D. Eff was the first collector to find the "heathii" form at two localities in Routt Co., Colorado, during July and August, 1953 (Fig. 3). I collected the first Wyoming specimens, from Carbon Co., in early August, 1977.

As noted by both Ferris and Fisher in the 1981 publications cited above, there is considerable phenotypic variation in both the Routt and Carbon Co. populations. Specimens from these areas are generally quite pale ventrally, when compared to typical *calanus godarti*, and many manifest the wide white band characteristic of the "heathii" aberration. In many, but not all, of the males, the forewing scent pad tends to be paler in color than in normal *godarti*.

Notwithstanding this variability, Scott (1981) has raised the "heathii" form status of these populations to subspecific recognition as the trinomial *S. calanus albidus* Scott. The designated type locality is "NW Hayden,





Figs. 1-2. Typical male of *Satyrium calanus godarti* from Hardscrabble Creek, Custer Co., Colorado, 4 July 1968, leg. J. A. Scott. **(1)** Dorsal. **(2)** Ventral.

Fig. 3. Ventral surface of *S. calanus* male from Rabbit Ears Pass, Routt Co., Colorado, 22 July 1972, leg. M. S. Fisher.

Routt Co. Colo." The original description of *albidus* neither figures nor describes the male Holotype *per se*, nor does it adequately discuss the pattern variation that occurs within Colorado and Wyoming populations. In fact, Scott does not mention at all that *calanus* even occurs in Wyoming. The female Allotype is from Montrose Co., Colorado, and paratypes are from Routt, Garfield and Montrose Counties. Delta Co. is also mentioned, but without specific locality.

## Study Site and Observations

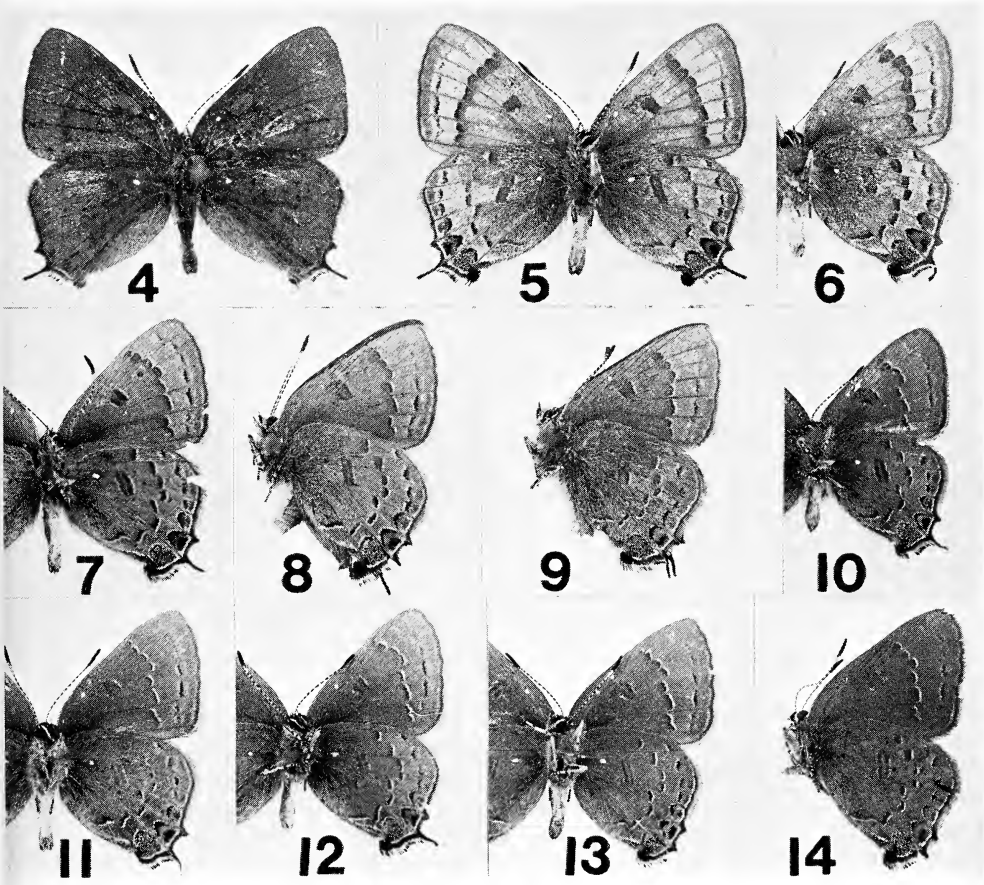
The remainder of this paper discusses the polymorphic nature of *S. calanus* from the vicinity of Battle Creek, ca. 7800′ (2380 m), Sierra Madre range, Carbon Co., Wyoming, and includes some comments about populations on the Western Slope in Colorado. These butterflies are not particularly common in Carbon Co. The first specimens were collected by the author in 1977, and the totals to date are only 28 males and 9 females.

Of the sample taken, a wider range of variation is observed in the males than in the females, as indicated by Figs. 4-14 (males) and Figs. 15-20 (females). This difference between the sexes may simply reflect the smaller female sample size. Dorsally, fresh specimens of both sexes are gray-brown as opposed to the dark brown to almost black of *godarti*. Ventrally the ground color in both sexes ranges from very pale gray (nearly white in some males) to pale gray-brown, as opposed to medium-to-dark brown in normal *godarti*. The males range from the typical "heathii" phenotype (Figs. 5-6) to forms resembling other subspecies of *calanus* in maculation, but not coloration (Figs. 11-14). Table 1 summarizes the frequency of various color forms found in the Carbon Co., Wyoming, and Routt Co., Colorado, populations.

The variation in the ventral maculation of the females is not so pronounced as in the males. Two specimens are of the form shown in Figs. 16-17, these being closest to "heathii" collected to date. The more usual female forms are shown in Figs. 19-20. Interestingly enough, "heathii" was originally described from a female specimen.

Specimens of *calanus* from along the Western Slope in Colorado are generally paler than Front Range *godarti*, and their maculation in general is reduced, including the hindwing "Thecla" spot. One specimen in the M. S. Fisher collection from Gunnison Co. is very white ventrally.

The Wyoming population occurs in oak-aspen-conifer habitat. The majority of the specimens collected have been taken along the top of a ridge where *Q. gambelii* is the dominant tree. The butterflies are flushed from the scrub by the traditional "beating" method. A few specimens of both sexes have been taken in a valley several hundred feet below the ridge, where they were nectaring at various flowers, but they do not appear to visit flowers on a regular basis. Both the ridge and valley area are aligned in a north-south direction, with the valley to the west side of the ridge. The



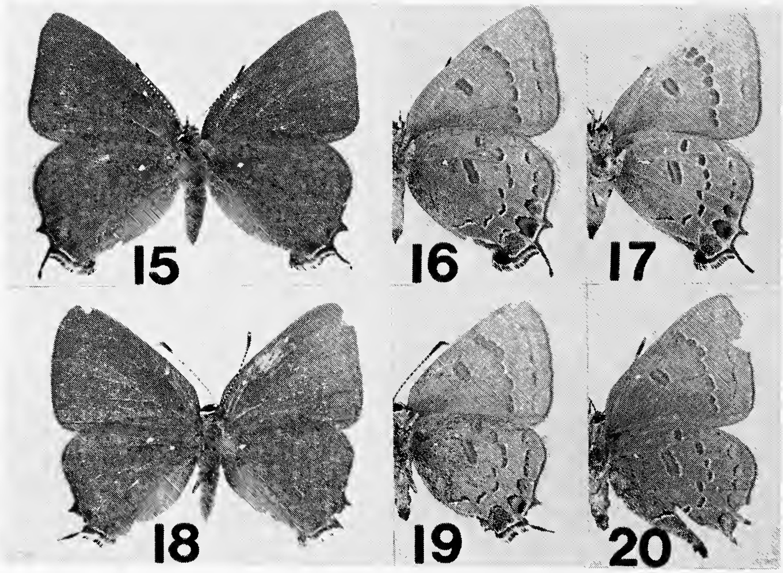
Figs. 4-14. Variation in males of *S. calanus* from vic. Battle Creek, west slope of Sierra Madre range, Carbon Co., Wyoming, ca. 7800′ (2380 m), all 29 July 1981, collected by the author. (4) Dorsal. (**5-14**) Ventral surfaces of ten specimens.

butterflies follow the sun, frequenting the eastern side of the ridgetop in the morning, and the western edge and slope in the afternoon.

The Routt Co. colony near Rabbit Ears Pass occupies a similar ridgetop habitat. The geographic extent of this colony and the Carbon Co. colony are both quite small.

## Discussion

*S. calanus* appears to occur in disjunct colonies along the Western Slope from southern Wyoming to southern Colorado. There is considerable clinal variation throughout this region.



Figs. 15-20. Variation in females of *S. calanus* from vic. Battle Creek, west slope of Sierra Madre range, Carbon Co., Wyoming, ca. 7800′ (2380 m), collected by the author. **(15)** Dorsal, 29 July 1981. **(16)** Same, ventral. **(17)** Ventral, 29 July 1981. **(18)** Dorsal, 2 Aug. 1977. **(19)** Same, ventral. **(20)** Ventral, 2 Aug. 1977.

Since Scott did not figure the Holotype of *albidus*, nor did he provide a description of it, this taxon is enigmatic. It is questionable that the Wyoming and related Colorado populations discussed above merit subspecifc recognition because of their variability, as I so stated (Ferris, 1981(82)). There is no difference in the male genitalia between the Wyoming population and typical *calanus godarti*. While Scott alluded to some variability of *albidus*, he did not exclude any variants from the type series (Art. 72(b), Code of the I.C.Z.N.). In view of the wide geographic range and disjunct populations represented by the type series of *albidus*, it is doubtful that this taxon satisfies the provisions of Articles 72 & 73 of the Code of the I.C.Z.N. Article 13 is also not met.

*Acknowledgments:* I would like to thank M. S. Fisher of Littleton, Colorado, for providing additional information on Western Slope *calanus*. Dr. Lee D. Miller, Allyn Museum of Entomology/Florida State Museum kindly read and commented on the first draft of this paper. Two anonymous reviewers further commented on the original draft.

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TABLE 1. Frequency of Ventral Phenotype in *S. calanus* from Carbon Co., Wyoming, and Routt Co., Colorado

| **Males** | | **Carbon Co. Wyoming (N = 28)** | **Routt Co. Colorado (N = 17)** |
|---|---|---|---|
| Pale Gray-White (= "heathii") | Figs. 3, 5-6 | 0.29 | 0.53 |
| Gray | Figs. 7-9 | 0.25 | 0.47 |
| Gray-Brown | Figs. 10-13 | 0.43 | — |
| Light Brown | Fig. 14 | 0.03 | — |
| **Females** | | **(N = 9)** | **(N = 0)** |
| Gray | Figs. 16-17 | 0.22 | — |
| Gray-Brown | Figs. 19-20 | 0.78 | — |

Note: Only one specimen of the "heathii" phenotype was collected at Beulah, Pueblo Co., Colorado. The "heathii" form is characterized by the ventral postmedian space being very much lighter than the ground color. This is a recurrent gene in many Eumaeine hairstreaks.

*Journal of Research on the Lepidoptera* 21(3): 194-198, 1982(83)

# On the Status of *Euphydryas editha baroni* with a Range Extension of *E. editha luestherae*

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**Abstract.** The subspecies name *baroni* has been misapplied to include all Coast Range populations of *Euphydryas editha* found north of the San Francisco Bay area. However, the original description and correspondence between the original collector, Baron, and the author of the species, Edwards, indicate that *baroni* should be restricted to a very few populations on the immediate coast of Mendocino County, California. It is suggested the subspecies name *luestherae* be applied to populations traditionally lumped with true *baroni* that inhabit Inner Coast Range chaparral.

## Introduction

More than a decade ago study of *Euphydryas editha* was extended from the well-known populations on Jasper Ridge (Ehrlich, 1965) in the Outer Coast Range of California to other locations where populations of different subspecies are found (Gilbert and Singer, 1973). Findings were in line with the view of Ehrlich and Raven (1969) that most species are neither ecological or evolutionary units. *Euphydryas editha* is made up of a number of ecotypes, groups of ecologically similar populations (White and Singer, 1974), which show similar allele frequencies at at least some gene loci (McKechnie et al., 1975; Murphy, Wilcox and Ehrlich, in prep.).

Within California, where local differentiation is greatest, ecotypes more or less match the named subspecies of *Euphydryas editha*. Coastal populations ovipositing on *Plantago erecta* are subspecies *bayensis*, Sierra foothill populations on *Collinsia tinctoria* are *rubicunda*, and so on. Some subspecies, as now applied, appear to be made up of several local host races in similar habitats—*monoensis* for instance includes populations ovipositing on *Collinsia* and *Plantago* in Ormsby County, Nevada and on *Castilleja* in Mono and Inyo counties in California.

To date *baroni* is the only subspecies name applied to *editha* from California north of San Francisco and west of the Central Valley. The vast majority of specimens originate from the inner Coast Ranges where *E. editha* flies in *Arctostaphylos*-dominated chaparral, ovipositing nearly exclusively on a hemiparasitic scroph, *Pedicularis densiflora*, and commonly nectaring on *Eriodictyon californica*. However, the California

Academy of Sciences recently acquired two specimens of *Euphydryas editha* from Pt. Arena, Mendocino County, California, collected on 9 June 1962 by Hardin B. Jones (see Fig. 1). The appearance of habitat surrounding Pt. Arena could not be more distinct from inland chaparral, and the extremely small, darkly marked individuals from there dramatically differ from Coast Range "*baroni*". Yet this is apparently not a new subspecies. It is my opinion that these two specimens are the "real" *baroni*, and that this name was never intended to refer to butterflies from chaparral areas.

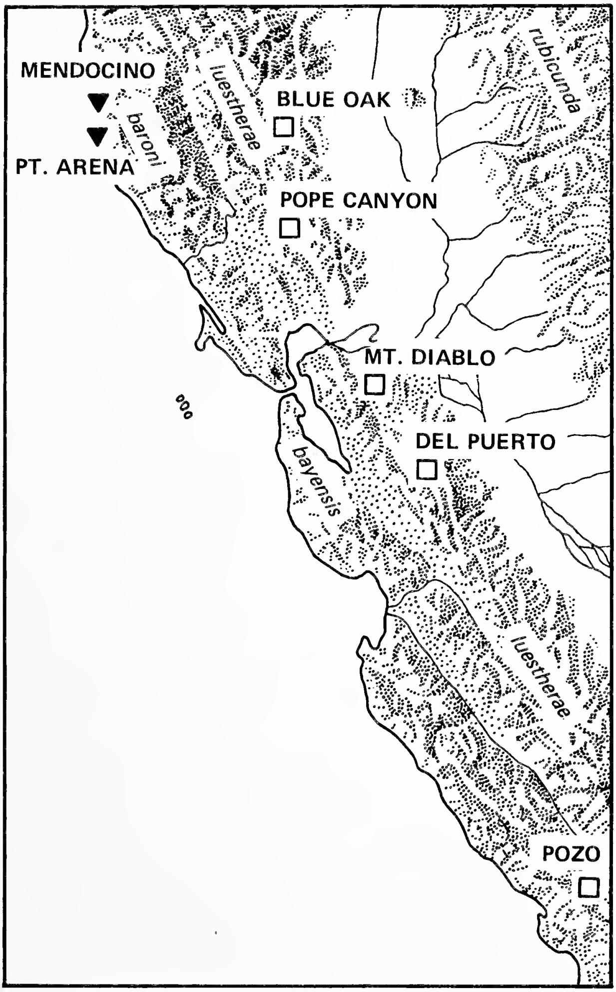

Fig. 1. Distribution of *Euphydryas editha* subspecies.

## Documentation

During December, 1878, William H. Edwards received from Oscar T. Baron a box of hibernating checkerspot larvae which hatched from egg masses laid the previous June 29th (Edwards, 1879, 1897). Though these larvae did not survive the winter, Edwards described the early stages (Edwards, 1879). In May of 1879, Edwards received chysalids of the same butterfly which Baron had reared from the same lot of larvae (Edwards, 1897). This is important in establishing the identity of *baroni* since F. M. Brown has assigned a lectotype for this subspecies from among adults emerged from those specific chrysalids. This designation was necessary to clear up a complex situation arising because Henry Edwards (1881) was the first to describe adequately the adult of *baroni*, and had been credited its authorship by many, including W. H. Edwards himself (see Brown, 1966 for details).

The type locality appears to have been assigned to Mendocino, California, on the strength of the postmark on the material shipped to W. H. Edwards. Yet Brown (1965) established that at the time the chrysalids were received by Edwards in West Virginia, May, 1879, Baron was well into a collecting trip east into the mountains of Mendocino and Lake Counties, where he also collected *Euphydryas editha*. However, preceding this journey Baron did not venture far, collecting locally where he worked in the town of Mendocino and nearby Navarro, both on the immediate coast (Brown, 1965). Combined with the knowledge that the 1879 adults were from larvae collected in 1878, a strong case is made for a coastal origin for *Euphydryas editha baroni*.

Additional information in W. H. Edwards' (1897) monograph indicates that Baron and Edwards considered *Euphydryas editha* from coastal and inland populations as distinct. They, in fact, discussed them as different species. Edwards (1897) quotes Baron ". . . I have the caterpillars of *rubicunda* and *baroni* side by side". . . and (*rubicunda*'s) "caterpillar is certainly distinct from that of *baroni* and feeds on different plants". Baron and Edwards use the name *rubicunda* mistakenly. They fail to distinguish Baron's inland Mendocino County populations of *editha*, from Eden Valley, Big River and near Ukiah, from the *rubicunda* of the Sierra Nevada foothills described by Henry Edwards (1881), which was then still rare in collections. Furthermore, the *Melitea rubicunda* illustrated by Edwards (1897) are Inner Coast Range *editha*, certainly not from the Sierra foothills, where dorsal wing surfaces are much redder. (The name *rubicunda* is controversial itself and may be a synonym for *E. editha editha* Boisduval, since the original collector of *editha*, Lorquin, did not venture as far south as the now-accepted type locality of *editha* [J. F. Emmel, pers. comm.].) Nonetheless, Baron and Edwards do not mix up coastal and inland *Euphydryas editha*; to them the inland butterflies were not *baroni*.

## Recommendation

Though northern California chaparral populations of *Euphydryas editha* are not *baroni*, there is a name which can apply. Murphy and Ehrlich (1980) described *Euphydryas editha luestherae* from ecologically similar populations from the chaparral of the Inner Coast Range south of the Sacramento River Delta. They noted that Napa and Sonoma County individuals were "... phenetically intermediate to *baroni* (sic) and this new subspecies (*luestherae*)." Preliminary electrophoretic evidence (Wilcox, Ehrlich and Murphy, in prep) comparing 20 loci coding for structural genes indicates that the genetic distances between and an extremely southern *luestherae* population, Pozo, San Luis Obispo County, and a northern population, Blue Oak Campground, Lake County, are no greater than between samples taken in different years from the same populations at Pozo or at Pope Canyon, Napa County. In fact, present genetic distances are greater between Pozo and Del Puerto Canyon, Stanislaus County, both originally assigned to *luestherae*, than between Pozo and all other Inner Coast Range populations that have been sampled from north of San Francisco Bay.

The northern range limits of *Euphydryas editha luestherae* therefore should be extended from Mt. Diablo, Contra Costa County, to include populations in Napa, Sonoma, Lake, Mendocino, Colusa, Glenn and Tehama counties, in other words all Coast Range populations which use *Pedicularis densiflora* as their primary larval host plant. The subspecies *rubicunda* should refer to populations ovipositing on *Collinsia tinctoria* south from Mud Creek, Butte County (near Chico), through the Sierra Foothills to Fresno County at elevations of 400-1400 m.

*Euphydryas editha baroni* is now restricted to populations on the immediate coast of central Mendocino County south from the vicinity of the town of Mendocino. *E. editha* from the extreme north coast of that county are phenetically distinct from *baroni* and probably have an affinity with *Plantago lanceolata*-feeding populations of southern Oregon (White and Singer, 1974) which may be *taylori*. In any case, Oregon records are not *baroni* (see Dornfeld, 1980).

An additional pertinent note: Dos Passos (1964) and Miller and Brown (1981) list a "transitional form" or aberration of *baroni*, "*dunni*", credited to Gunder (1929). The holotype is in the American Museum of Natural History. Three labels in Gunder's handwriting below this specimen read—*Label 1*-Mendocino Co., Calif. 1912, (W. F. Eastman), received thru Mr. Norman R. Gunn. *Label 2*-described in the Pan-Pac. Entom., July, 1929-(gunni is mispelled [sic] in the orig. description). Holotype male, collection of Jeane D. Gunder. Euphy. editha Bdv., race baroni Edw., tr.f. *gunni*, J. D. Gunder. *Label 3*-J. D. Gunder collection, Ac 34998. It is impossible to ascertain from these locality data or from the individual's phenotype whether *gunni* is actually an aberration of *baroni*, of *luestherae* or of yet some other subspecies.

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# A Melanic Male Aberration[1] of *Papilio glaucus canadensis* from Northern Wisconsin

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Melanic male specimens of *Papilio glaucus canadensis* Rothschild and Jordan have been described from northern Wisconsin (Forest County) by Ebner (1960) and from the vicinity of Nipigon, Ontario, Canada by Sicher (1962). Similar male specimens of *Papilio glaucus* have been reported from Markham, Ontario, Canada (Johnstone, 1978), Penland, North Carolina (Rosier, 1977), and the Great Smokey Mountains National Park, Tennessee (see Brewer, 1980). Similarly-colored specimens which could be females have been reported from West Virginia (Drees, 1978) and by Walsten (1977), although it has been suggested (Clarke, 1978) that these specimens may in fact be male mutants rather than semi-melanic females

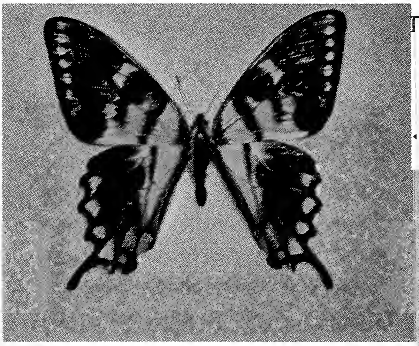

Fig. 1a. Melanic male aberration of *Papilio glaucus canadensis*. Upperside

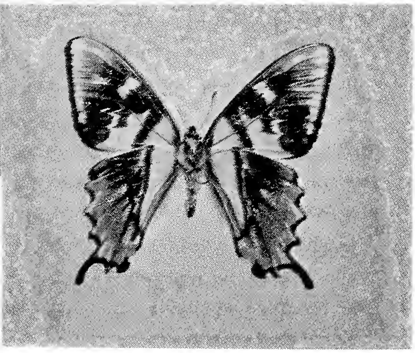

Fig. 1b. Same as Fig. 1a. Underside

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[1] This specimen is presently located in 240 Russell Laboratories, University of Wisconsin and will be deposited for permanent reference in the Milwaukee Public Museum (Invertebrate Zoology section).

or gynandromorphs (with partial male and female characteristics).

These kinds of aberrations are probably not related to the dimorphism (black and yellow forms) in females of *P. glaucus glaucus* L. (Clarke and Sheppard, 1959; Shapiro, 1981) although a clear yellow patch (of various size and shapes) near the post-median discal area of the forewings, which is characteristic of essentially all of the previously mentioned melanics has also recently been observed in aberrations of melanic females of *P. glaucus glaucus* (Scriber, Ritland, Evans, in prep.; see also Edwards, 1884).

On 2 June 1980 a melanic male *P. g. canadensis* specimen was captured from amongst 100-200 swarming butterflies (of a disturbed puddling group) near the University of Wisconsin Pigeon Lake Biological Field Station (Sawyer County, Wisconsin). Our specimen (see Fig. 1) is very similar to that captured two counties eastward by L. Allen in 1958 (figured in Ebner, 1960). The upper and lower surfaces of the hind wings are rather spectacular in the amount of blue and orange coloration, and might at first be mistaken for an unusual female. As is the case with other melanic male aberrations reported above, there is a clear yellow patch near the discal area of the forewings. We assume the subspecies to be *canadensis*, because Pigeon Lake is well north of the limit of *P. g. glaucus* in Wisconsin (see Scriber *et al.*, 1982).

Our capture of this melanic aberration and the capture during the same year of a very similar melanic male *P. g. canadensis* by Joel Trick near Green Bay in (Oconto County) Wisconsin (Walt Gould, pers. comm.) suggests that this bilaterally symmetrical color pattern may not be as uncommon as once generally believed. However, it is unknown if these choice Wisconsin specimens are representatives of additional individuals in the population with the same genetically-fixed traits, or if they represent products of spontaneous mutations or environmental effects.

A literature search through the latter half of the 19th century yielded three records of male aberrations virtually identical to the one we figure. The first such specimen was captured in July, 1888 by Robert MacKenzie at Collins Inlet eighteen miles east of Killarney, Ontario, and is figured by Fletcher (1889). Another similar male was collected from Orillia (near Simcoe), Ontario by C. E. Grant (1896). A third such specimen captured by A. Ronke in Elizabeth, New Jersey in 1899 was described by S. T. Kemp (1900) who also suggested that such specimens have a distinct name (*Papilio turnus* ab. *fletcheri*) in honor of the first individual to describe the type. Except for Mecky Furr's Tennessee male (see Brewer, 1980), all of the specimens described from more northern areas (i.e. within the potential range of *P. g. canadensis*) are strikingly similar and apparently very stable through space and time, suggesting maintenance as a low-level polymorphism.

*Acknowledgment.* Collection of this specimen was made possible by a grant from the National Science Foundation DEB-7921749 (to JMS). We thank Mark Evans

for the photography and an anonymous reviewer for useful comments.

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## Notes

### On the Behaviour and Flight Patterns of the Neotropical Butterfly, *Anartia fatima* Fabricius (Nymphalinae)

Local movements by insects must allow efficient use of different habitat components, especially where areas for mating, adult foraging and larval development do not coincide precisely (e.g. Gilbert, L. E. & M. C. Singer. 1975. Butterfly ecology. Ann. Rev. Ecol. Syst. 6:365-397). This paper reports the flight behaviour of *Anartia fatima.*

*A. fatima* flies over many types of cleared terrain in Central America. A study, from 21 to 24 July 1979, was made at 1250 m in Chiriqui Province of the Republic of Panama, and at sea level in Corcovado National Park in Costa Rica, 3 October 1981, both during the wet season. The Chiriqui colony occupied about 1.5 ha of a coffee plantation, the butterflies frequenting the grassy and weedy areas between rows of bushes. At Corcovado they occurred in a scrubby pasture, grazed by ponies, and surrounded by second growth scrub.

Females were followed and their behaviour noted. During half hour periods, the number of flowers visited, eggs laid and interactions with other *A. fatima* were recorded. The number of flights, and their distances, were recorded (measured by pacing or with a ruler; many flights shorter than 0.2 m were not measured to avoid disturbance). The direction of each flight for females (at Corcovado) was assigned to one of 8 equal sectors (each of 45°). For analysis, butterflies were counted as flying straight on if successive flight directions fell into the same or one of the two adjacent sectors, and as changing direction if into any of the five other sectors.

All flights were assigned to one of three categories: foraging flight during and between adult feeding periods, oviposition flight during egg laying periods and displacement flight, comprising all remaining flights (see Table 1).

1. Foraging flight. Many short flights (80% unmeasured), whilst flitting between flowers.

2. Displacement flight. Long flights (all measured) used to commute between foraging, resting and oviposition areas. The flight was directed (more flights straight

Table 1. Flight characteristics of female *Anartia fatima*

| Flight Type | Number of Measured Flights | Distance per Measured Flight in Metres Mean | S.D. | Number of Unmeasured Flights | Proportion of Flights Straight on |
|---|---|---|---|---|---|
| Foraging | 41 | 1.6 | 1.7 | 176 | 28/47 (60%) |
| Displacement | 58 | 8.4 | 9.2 | 0 | 38/45 (84%) |
| Oviposition | 121 | 1.7 | * | 0 | — |

*: S.D. not estimable as not all flights measured separately—range of 15 flights (including longest) 0.15-20.0 m.

on than whilst foraging $X^2 = 5.92$; $p < 0.05$). Displacement flight was faster than the other two categorized, and at steady height (1.0 to 1.5 m) above the ground for long distances.

3. Oviposition flight. Many intermediate length flights (all measured). This flight partly consisted of agitated fluttering, landing for just a second or two on many occasions. Flight high relative to length (up and down).

*Mate location and rejection.*—Male *A. fatima* fly actively in search of mates (patrolling sensu Scott, J. A., 1974; Mate-locating behavior of butterflies. Amer. Midl. Nat. 91:103-117), which it has been suggested conforms to a zigzag pattern (Emmel, T. C., 1972; Mate selection and balanced polymorphisms in the tropical nymphalid butterfly, *Anartia fatima*. Evolution 26:96-107). At Corcovado four males were followed. Whilst flying (20 out of 53 minutes), they encountered 33 other males and 12 females, a faster encounter rate than when settled, when 22 other males and no females were intercepted in 33 minutes.

Females often rejected males by closing their wings sharply and positioning their undersides at right angles to the approaching suitors, thus obscuring the pale band on their upper surfaces, which Emmel (1972) showed to be attractive to males. In 9 of 10 cases when a male intercepted a flying female, she landed and then adopted the rejection posture, on the tenth occasion the female flew on, and after a brief chase the male left. More commonly in other species the female's wings are spread, and usually vibrated, and the abdomen raised to preclude copulation. Female *Mellicta athalia* Rott. (a European Nymphalid) initially snap their wings shut when males or other large insects fly past, only adopting the raised abdomen posture if the male comes very close (C.D.T. pers. obs.). When female *M. athalia* close their wings, they become less visible and may avoid detection by unwanted males and potential predators. *A. fatima* appears to have developed this simple avoidance into a distinct rejection posture. Scott, J. A. (1973; The mating of butterflies. J. Res. Lepid. 11:99-127) recognised various rejection postures, but data for *A. fatima* was not included.

*Behaviour sequence and flight patterns.*—At Chiriqui, a single female was followed from 10.05 to 13.16 (Fig. 1). Having fed on a patch of flowers for 50 minutes, she moved away from them onto grass and subsequently to a coffee bush, on which she reted. After resting she resumed activity and started to oviposit in a more shaded area, laying about 75 eggs, before being lost at 13.16. By this time it has started to drizzle, the rain becoming heavy by 13.30, after which no more activity by any *A. fatima* was seen.

Two females were followed at Crcovado. Both started by feeding, followed by a period of considerable movement, one of them then resting, having moved from where it was nectaring. Unfortunately, both butterflies were lost before engaging in other behaviour, flying out of the study field over the surrounding scrub, but probably would have started to oviposit as both had become agitated (see oviposition flight) and one had commenced crawling on the ground. At Chiriqui the female laid eggs low on the vegetation and litter, having first crawled over it.

The frequency of courtships by males increased towards the end of the feeding period, after which the Chiriqui female moved out of the flower-rich area (where most males were) and the number of courtships decreased. At Corcovado, where nectar sources were more evenly distributed, females did not escape the attentions of males so effectively when they moved from where they had been feeding. At San

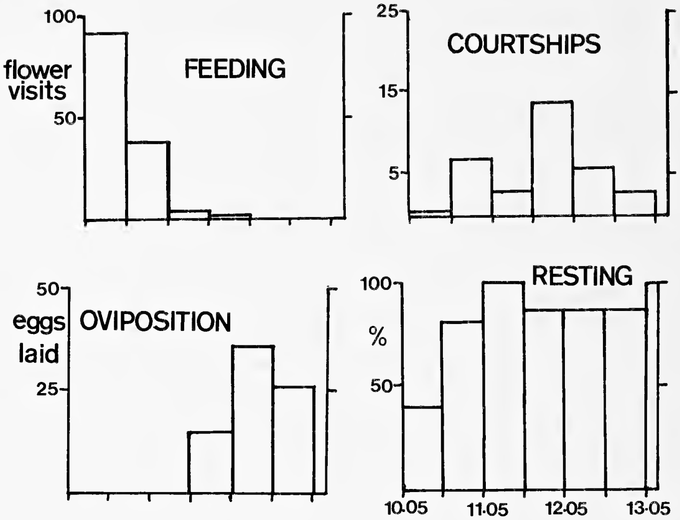

Fig. 1. Behaviour sequence of a female *Anartia fatima*, showing the number of flowers visited (n = 134), the number of courtship attempts by males (n = 34), the number of eggs laid (n = 75) and the percentage of minutes in any half hour when resting was observed.

Vito in Costa Rica (similar altitude and climate as Chiriqui site) Emmel (1972) found that male activity peaked mid to late morning.

Wicklund, C. (1977; Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of *Leptidea sinapis* Lepidoptera. Oikos 28:56-68) found that the pierid *L. sinapis* L. followed a sequence of feeding then ovipositing; the females were observed to feed on flowers in woodland and then to move out into a meadow to lay. Movements between adult feeding and larval development areas have also been described for *Euphydryas editha* Boisduval (Gilbert, L. E. & M. C. Singer, 1973; Dispersal and gene flow in a butterfly species. Amer. Nat. 107:58-72).

The displacement flight was longer and more straightened out than foraging flight, permitting travel between different habitat components, whereas foraging flight was appropriate to feeding in restricted flower patches. The behavioural sequence and flight patterns suggest that distinct responses to habitat components allow butterflies to utilize resources efficiently.

*Acknowedgments.*—This study was carried out on the Cambridge Butterfly Expedition to Central America and the Cambridge Hummingbird Study Expedition (C.D.T. only). We are very grateful to all who assisted and sponsored them, particularly Sr. Ratibor Hartmann (Chiriqui) and the Costa Rica Park Service (Corcovado) on whose land the work was conducted. Thanks also to Robin Baker, Tom Coaker and Sally Corbet for valuable comments on the manuscript.

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## Notes on *Tomares mauretanicus* (Lycaenidae) in Morocco

*Tomares mauretanicus* is a little known hairstreak, endemic to Africa north of the Atlas mountain ranges. The purpose of this note is to record some observations, made in Morocco during 1981 and 1982, which may be of interest to students of the Theclinae. *T. mauretanicus* occurs throughout Morocco, flying in early spring—February to March in the lowlands, during April at higher levels e.g. near Azrou (Middle Atlas) and Asni (High Atlas). Populations are usually diffuse, but may on occasion reach high densities where the leguminous foodplant abounds. Strict habitat selection was observed near Asni (1200 m); butterflies were seen only in open areas, where the host *Hippocrepis multisilquosum* grows, and not in interspersed areas of young, commercially planted trees. *T. mauretanicus* was never seen to enter even light shade. Population numbers in any area seemed to be related to the density of *H. multisiliquosum*. The closely related congener *T. ballus* (which is normally recorded from different leguminous hosts (Higgins and Riley, 1980; A Field Guide to the Butterflies of Britain and Europe. 4th Ed. Publ. W. Collins Sons & Co., Glasgow) also occurred around Asni during March-April, but at low densities and with a distinct tendency to occur in more shaded sites. No evidence was found for either larval competition or mating interference between the two species.

Male *T. mauretanicus* flew towards and 'investigated' free-flying conspecifics. One successful courtship was observed when a contacted female settled and immediately closed her wings. The male continued to flutter for a few seconds, landed behind the female, and after a few more rapid flutters, initiated copulation. Time elapsed from first contact to the onset of copulation was less than 30 seconds. The position adopted for mating (Fig. 1) is one with the wings of both sexes tightly closed and directed at an angle to those of the partner.

Fig. 1. Copulating pair of *Tomares mauretanicus*. Note oblique slanting of the wings. Female to the right.

Mated female *T. mauretanicus* flew low over the vegetation searching for hosts. On contacting a *Hippocrepis* individual, females spent a considerable time crawling over the surface of the legume, apparently searching for optimal oviposition sites. Detailed studies were made of oviposition choice, and will be presented elsewhere. Notably, females appeared to select small individuals of the host, with few or no mature flowers. Oviposition on immature hosts may anticipate growth of the plant for maturing larvae. Like many other butterflies, females also distributed most eggs on those individual hostplants most isolated from conspecifics. Such egg distributions have been argued to be the outcome of searching patterns, where isolated plants are more frequently encountered by a female (Courtney & Courtney, 1982; The 'edge-effect' in butterfly oviposition: causality in *Anthocharis cardamines* and related species. Ecol. Ent. 7:131-137).

Eggs were distributed predominantly on the buds and young leaves of growing plants. The white eggs appeared to develop a black spot in the central depression as they matured. Unusually for a Hairstreak, the eggs were often laid in small batches, with up to 6 eggs of identical age placed closely together. More isolated plants were found to have bigger egg batches. No effect of plant size on egg batch size was found. Some larvae were found or reared. They have the typical squat hairstreak form, with a greenish ground colour, lateral stripes of yellow and purple and a dorsal stripe of purple within two yellow bands.

Some of the colonies of *T. mauretanicus* found are in non-agricultural areas which are used only sporadically for grazing. By far the majority of populations are associated with agricultural areas, where *H. multisiliquosum* occurs as a casual weed or as an invader of fallow land. Whilst present land practices continue, the future of host and butterfly populations seems secure. However with increasing use of herbicides and pesticides in lowland areas, and persistent overgrazing by pastoral flocks in some upland areas, some decrease in numbers of this attractive and unusual hairstreak is to be expected.

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## An Effect of the Colony Edge on Gatekeeper Butterflies, *Pyronia tithonus* L. (Satyridae)

How are the boundaries of discrete butterfly colonies maintained? Gatekeeper butterflies, *Pyronia tithonus*, were studied in a herb-rich unimproved pasture in west Dorset, England, in 1980. The site was divided into 20 m by 20 m quadrats. When a butterfly was encountered in a quadrat it was followed for two minutes or until it left that quadrat, whichever was the shorter. The direction taken by butterflies leaving quadrats was noted (i.e., into which of the adjacent quadrats).

One hundred twenty butterflies were followed in 7 quadrats. Males tended to leave quadrats more frequently than females (43/60 males versus 33/60 females; $X^2 = 2.91, 0.05 < p < 0.1$) which may be attributable to their mate searching activities. Both sexes preferentially flew towards the centre of the old meadow when they were near its margin (75 flew across 20 available quadrat edges towards or within the meadow versus only 1 flying across 8 available quadrat edges away from the meadow; $X^2 = 26.3$, $p < 0.001$). No individual flew into or over the adjacent wood and only one butterfly flew from the old meadow into an adjacent field sown to grass (*Lolium multiflorum* Lam). However, gatekeepers occasionally did fly into this sown pasture to nectar on *Cirsium vulgare* Ten. (Compositae), but none of such nectaring butterflies encountered were observed to fly out further into the sown pasture, and 11 flew back into the old meadow.

The gatekeepers' mobility would seem to permit the colony to disperse without the tendency to keep within the old pasture. The behavioural mechanism by which they remained confined to the old pasture was not investigated. The woodland margin is distinct, but the old meadow/sown pasture boundary is more subtle. There were more flowers available, longer turf, more available foodplants, and a greater adult butterfly density in the old meadow than in the sown pasture. Gatekeepers could be reacting to any or a combination of these, but experimental manipulation of density, sex ratio, and habitat quality is needed if these factors are to be distinguished.

*Acknowledgments:* My thanks to Tom Coaker, Sally Corbet, Mark Cheverton and an anonymous reviewer for helpful comments on the manuscript.

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## Hide and/or Seek

James A. Scott's note on "Mate-Locating Behavior of *Gnophaela latipennis vermiculata* G.&R." (J. Res. Lepid. 20:51) raises the question of whether nectaring solitaries are unmated females. Inasmuch as these Pericopids are reported to visit yellow or white-flowered Composites during the afternoon, my own experiences on Big Pine Key, Florida, with the Syntomid *Syntomeida epilais jucundissima* Dyar, nectaring during the same time of day on the Composite *Flaveria linearis* Laq., suggest a possibility which might make mating safer for even aposematic animals. These slow-flying Syntomids are so conspicuous that their local name is "Uncle Sam Bug." Yet the gunmetal-blue moths are curiously hard to see against the yellow flowerheads on which they nectar when the sun is getting low. Partly because of corymb density, shadows in the yellow flowerheads soon deepen to blue, and sporadic openings are matched by translucent wingspots. (The sympatric Pericopid *Composia fidelissima vagrans* Bates, colored like the Syntomid, with the same Apocynaceous larval hostplants, and also with the same tendency to afternoon flight, nectars differently at least when both moths happen to be numerous.)

Whether the colors of shadows can protect nectaring solitaries from predators other than lepidopterists, or will protect copulating pairs from interfering conspecifics or mimics during a population crash is an interesting question. But surely in many Rocky Mountain "moist valley bottoms" shadows would lengthen early as in subtropical flatlands. Even if individual *G. l. vermiculata* are aposematic when flying, mating pairs may be facultatively cryptic if the yellow or white Composites on which they rest prove to transmit afternoon light as effectively as the moth's open wingpattern would suggest.

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## Book Reviews

*Systematics and Biogeography: Cladistics and Vicariance.*
Gareth Nelson and Norman Platnick. 1981. 567 pages. Columbia University Press, New York. Price: $36.80.

This book has broad application to Lepidoptera although they are not specifically mentioned. It is an important contribution to taxonomy and biogeography that interprets new developments in continental drift (= plate tectonics) in the light of cladistics (= phylogenetic systematics). In so doing, the works of Croizat (1964, *Space, Time, Form: the Biological Synthesis*) and Henning (1966, *Phylogenetic Systematics*) are freely drawn upon. Some biogeographic truths emerge, while more problems are raised than are solved.

Faithful readers of recent *Systematic Zoology* issues should be able to follow the extensive cladogram discussions. Cladograms' superiority to phylogenetic trees is slight (see pp. 142-147, 199-219, etc.), since these differ little in principle. Without the benefit of cladograms, biogeographic syntheses of Darwin, Wallace, Darlington, and Croizat are still useful in performing tests of various plate tectonic theories, of course. Chapter 2 reviews the history of branching diagrams, from Theophrastus to numerical taxonomy and cladograms.

Biogeography was once the pathfinder for geology via the landbridge theory, whereas today geology is pointing the way for biogeography via continental drift. Landbridge theory and massive over-sea dispersal were natural outgrowths of the days of permanently-fixed continents. Gondwanaland emerges as the place of origin and initial radiation of the modern biota, largely in coevolution with flowering plants.

They suggest a reappraisal of interrelationships of the Sclater-Wallace earth divisions from the viewpoint of continental drift and earth expansion (Chapters 6-8). The authors disagree with the concepts of "ontogeny recapitulates phylogeny" (Chapter 5) and "center of origin" (Chapters 6, 8). They note that historical geology has now joined forces with historical biogeography.

Center of origin and dispersal directions can be determined from cladograms. Of Cain's rules in recognizing centers of origin, the valid ones appear to be the greatest differentiation of a type, continuity and convergence of lines of dispersal, and direction indicated by geographical affinities. Using cladograms (figs. 8.9 and 8.11), Brundin found that in chironomids (Diamesinae and Podonominae), Australia and South America were more closely related than either is to Africa, with the most primitive species in southern Africa, also supporting certain Gondwanaland reconstructions. His cladogram pattern indicates an African origin with subsequent dispersal to South America and finally New Zealand and Australia. Darlington has found that radiation of animals from someplace in the Old World tropics is the common pattern.

An early development of moth families (Agaristidae, Noctuidae, Uraniidae) from the Castniidae of East Africa and Madagascar (Seitz, *The Macrolepidoptera of the World. vol. 14. The African Bombyces and Sphinges*, pp. 15-18, 1930) again points to Africa as a possible center of origin. Butterflies too may have first evolved in Africa (Smart, *The Aurelian* 1 (1):1-10, 1 (3):12-13, etc., 1978). However, angiosperms are probably tri-phyletic from woody Bennettitales, with Palmae in northwestern South America from *Sanmiguelia* (Colorado, Middle to Upper Triassic) producing monocots and Trochodendraceae in Assam and SW China and Compositae (Tree Senecios) surrounding Lake Victoria (Africa) producing dicots, based on butterfly and castniid host plant and phylogeny relationships (Shields and Perkins, in prep.).

Butterflies in common between Madagascar and the Oriental region (Corbet, *Trans. Ent. Soc. Lond.* 99:589-607, 1948) can be more readily explained by joining India and Madagascar in the past (Shields, *J. Geol.* 85:236-242, 1977). A few studies have appeared to date that discuss in some detail butterflies and continental drift (Hering, *Archiv fur naturgeschichte*, Berlin 87A (4):248-296, 1921; Stempffer, *Bull. Soc. Ent. France* 38:325-328, 1933; Eliot, *The Entomol.* 79:225-228, 1946; Holloway, *Biol. J. Linn. Soc.* 1:373-385, 1969; Eliot, *Bull. Brit. Mus. (Nat. Hist.), Ent.* 28:371-505, 1973; Shields & Dvorak, *J. Nat. Hist.* 13:221-250, 1979).

The book is liberally illustrated, well-organized, has select references, and author and subject indices. Hopefully this new union of phylogeny and plate tectonics may stimulate a renewed interest in Lepidoptera biogeography in the near future.

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*Animal Identification: a Reference Guide. Volume 3: Insects.*
D. Hollis (ed.). 1980. British Museum (Natural History), London and John Wiley & Sons, New York. viii + 160 pp. ISBN 0471-27767-3. Price: US $39.95.

This book, along with "Volume 1: Marine and brackish water animals" and "Volume 2: Land and freshwater animals (not insects)" both edited by R. W. Sims, is a guide to the identification literature. The book meets its objective of providing "a list of primary references which will enable non-specialists to set about identifying insects from any part of the world." Literature was selected, primarily by the British Museum entomologists, on the basis of usefulness in identifications, and especially the inclusion of keys, illustrations and bibliographies. Literature treating only one genus or species-group was excluded.

The references are arranged taxonomically, then geographically, making retrevial efficient. An index of group names is also provided. Many of the citations include helpful annotations on content or usefulness. Citations of some multi-part works have been combined to save space; this practice could have been followed more extensively (e.g. Diakonoff's Microlepidoptera of New Guinea on p. 123).

The Lepidoptera portion (pp. 120-137) seems well done and relatively complete. The only significant error I noticed (p. 128) is that Adamczewski 1951 should be listed under Pterophoridae not Aluctidae. The useful *Economic Insect Fauna of China* series was overlooked (understandably due to its rarity outside the People's Republic of China); it includes Lymantriidae, Noctuidae, Notodontidae, Pyralidae, Sphingidae, and Tortricidae. Other useful papers that could have been included are Davis 1967 (Nearctic Prodoxinae), 1975 (Ochsenheimeriidae), Freeman 1958 (Nearctic Archipinae), 1967 (Nearctic conifer leaf-miners), Hogue 1963 (Nearctic Stiriini), Kuznetsov 1979 (Palearctic Gracillariidae genera), McDunnough 1928 (Nearctic Agrotinae genera), Powell 1969 (Nearctic Adelinae), Rindge 1949 (many papers on New World Geometridae), and Shaffer 1976 (Neotropical Peoriinae).

The book will be very helpful to anyone faced with identifying insects in groups or from regions with which he is not familiar. However, it demonstrates the great lack of useful identification works for many taxa. As is common today, the price is quite high, especially considering the book has no illustrations.

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### *Butterflies of Oman*

Larsen, T. [B.] & Larsen, K., 1981. ca. 20 x 24 cm; 80 pp., 107 unnumbered col. figs. Published for the Government of Oman by J. Bartholomew, Edinburgh. Price: £ 6.00, hardback.

It is not always easy to review a book written by a friend. It is even more difficult in this case as the aim of the 'Butterflies of Oman' is both to give an easy written account of the butterflies for the naturalist and to summarize our present knowledge of the Papilionoidea and Hesperiidae of the Sultanate of Oman for the lepidopterologist. As a scientist I would naturally expect a somewhat more concise and yet more comprehensive account, with the general introductory chapter left out; those readers who have only basic knowledge of butterflies may find it fascinating. This chapter ('About butterflies') is followed from p. 19 by a faunistic account of the Papilionoidea and Hesperiidae species recorded in Oman, with notes on their distribution, ecology, taxonomy, biology, early stages, etc.; a clear separation of the two parts would have been advantageous. Every species is illustrated in colour; set specimens were photographed by the British Museum (National History), London and the photographs of habitats, living butterflies and their larvae were taken mostly by the authors. The overall quality of the colour illustrations leaves something to be desired (partly poor printing?) and both the shadows and the far too penetrating blue ground colour chosen for the set specimens seems to have a somewhat disturbing effect. The strong matt paper is well chosen as it excludes all unwanted reflections of light that could obscure the view of the reader. It would have been better to provide all illustrations with numbers. The senior author informed me that the above given citation of the authors' names is correct: the statement made in the book is not unequivocal and could well imply that the text was written by T. [B.] L. and design made by K. L. Perhaps a relevant remark that simple is beautiful is not entirely uncalled for. The authors did not have an easy task and their aim to extend what originally had been planned as a simple colourful book on the butterflies far beyond this did not make it easier. Their personal acquaintance with Oman enabled them to make numerous interesting observations on the Oman species in their natural environment. It seems that the authors managed to achieve their aims. And, above all, I am sure that many readers will appreciate their book.

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Editor's note: The region covered by this book has a unique characteristic perhaps not realized by many western hemisphere readers. Oman represents a trisection of the Palearctic, Ethiopian, and Oriental regions which is reflected in the butterfly fauna. Anyone concerned with broad issues of biogeography would find this work, in addition to its predecessor (T. B. Larsen, 1977, The Butterflies of Eastern Oman and their Zoogeographic Composition, The Journal of Oman Studies Special Report: 179-208) invaluable references.

**Errata—Book Review:** The review of Feltwell [*et al.*], 1981, *Large White butterfly: The biology, biochemistry and physiology of Pieris brassicae (Linneus)*, published in this journal 20(4), 1981(82), pp. 251-252, was written by Otakar Kudrna, Rhenusallee 30, D-5300 Bonn 3, West Germany.

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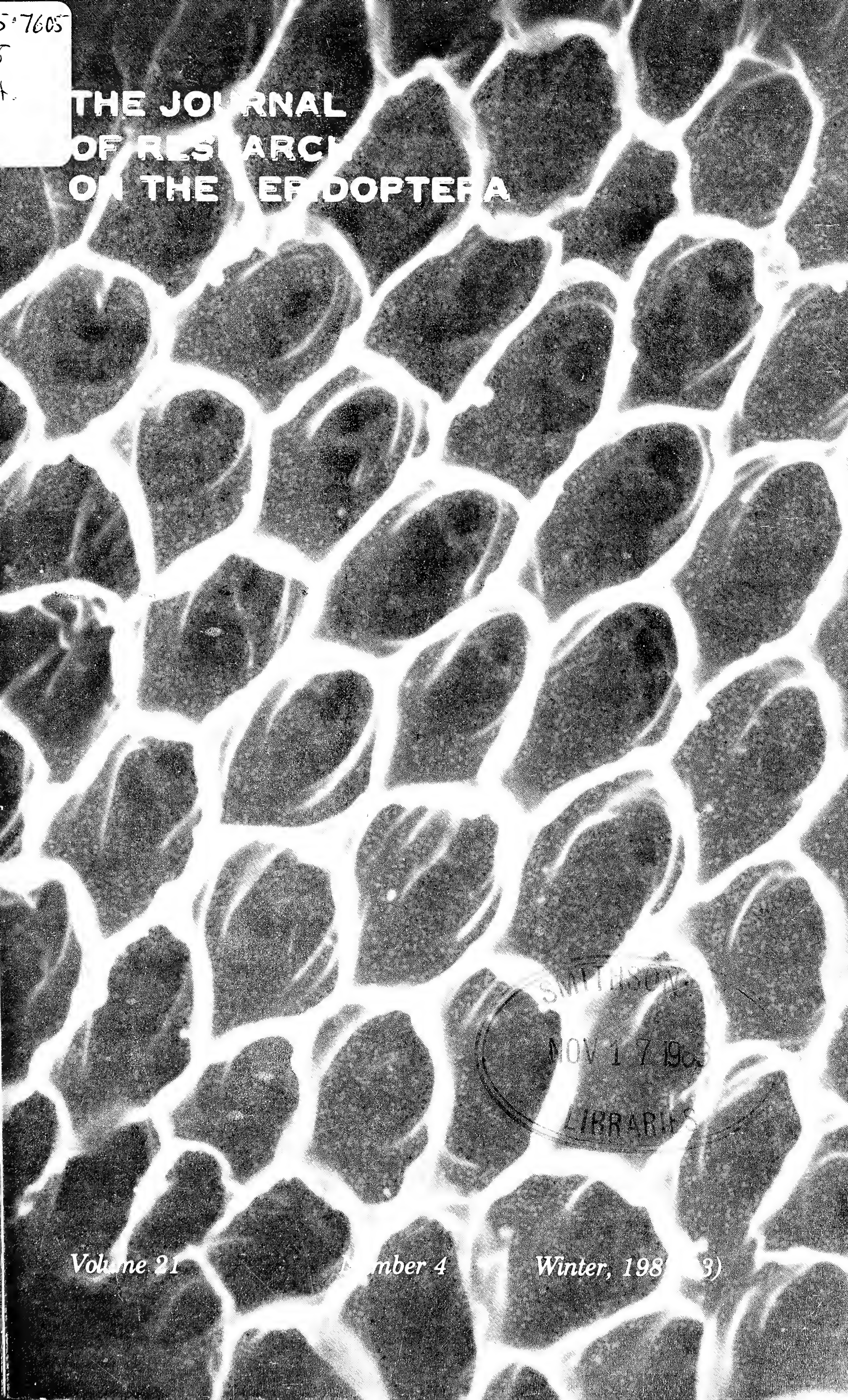

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## Announcement: Holarctic Lepidopterists Union

Madrid: May 24, 1983. During the course of a pleasant dinner at Horno Santa Theresa a proposal was made to form the Holarctic Lepidopterists Union. Present at this initial informal meeting were M. Gomez Bustillo, Paul R. Ehrlich, Rudi H. T. Mattoni and Dennis D. Murphy. Dr. Gomez Bustillo was unanimously selected as Chairman of the ad hoc union. It was agreed this evening that communication among Lepidopterists is in an abysmal state due to two reinforcing factors—1) the lack of exchange between European and American workers and 2) the recent appalling instability of butterfly nomenclature which is occurring in both the Palearctic and Nearctic regions.

The major long term objective of the union will be the development of a catalog/checklist of the Holarctic butterfly fauna with distribution data. Furthermore, the union will urge the application of a conservative nomenclature and restraint in creating new entities in the region until there is better understanding of relationships among extant taxa. Increased communication among all workers concerned with the region will be emphasized, and a consensus sought among participants through debate and consideration. A list of initial participants is in preparation, however, the union will be open to all interested parties. Communication will be mediated through a newsletter of this journal, including announcement of specialist listings and presentation of provisional checklists of specific groups as these are developed.

A first priority will be establishment of a tentative list of specialists and agreement on the defined boundaries of the holarctic. Emphasis will be on the truly holarctic derived fauna and not an exact geographic border. Obviously, no exact border definition can be completely satisfactory as broad transitions are found both in Mexico and Asia. The fauna of the border areas may be treated in addenda, as the relationships and interdigitation of groups at these borders is particularly fascinating; e.g. see *Butterflies of Oman* by Torben Larsen which describes the fauna of an area with intermixed Holarctic, Ethiopian, and Oriental faunal elements.

Since the increasing interest in butterflies as organisms for use in investigations of general principals of biology has coincided with a time of particularly poor communication among systematics workers and an attendant nomenclatural disarray, the objectives of this union are timely. Appearance of provisional lists should illuminate systematic deficiencies as well as agreements and disagreements in our view of the relationships among these organisms. Although efforts of the union may proceed slowly, a start is needed.

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# Taxonomic Uncertainty, the Biological Species Concept, and the Nearctic Butterflies: a Reappraisal after Twenty Years

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**Abstract.** In 1961 Paul Ehrlich surveyed the Nearctic butterfly fauna in order to demonstrate that the biological species concept had "outlived its usefulness." A reappraisal of two genera, *Lethe* and *Pieris (sens. lat.)*, after twenty years leads to the conclusion that the biological species concept is still very useful in both systematics and evolutionary biology.

> The true understanding of the Atus of Tahuti, or Tarot Trumps, also awaits full understanding. I have satisfied myself that these twenty-two cards compose a complete system of hieroglyphs representing the total energies of the Universe. In the case of some cards, I have succeeded in restoring the original form and giving a complete account of their meaning. Others, however, I understand imperfectly, and of some few I have at present no more than a general idea.
>
> *The Confessions of Aleister Crowley.*

Twenty years ago Paul Ehrlich asked himself "Has the biological species concept outlived its usefulness?" and answered "Yes." He bolstered his argument with a breakdown of the genera of Nearctic butterflies (Ehrlich, 1961), according to the purported ease with which distinct species could be recognized in them. Finding that a majority of the Nearctic genera included at least some ambiguous cases, he concluded that "at least at the present level of knowledge, the prevalence of the clearly defined species is a myth. . .the very nature of the biological species definition makes its use impossible in practice." This was strong language in 1961; it still is. It was echoed in a powerfully-argued paper in *American Naturalist* by Sokal and Crovello (1970). They did not use or cite Ehrlich's butterfly survey, but their conclusions were the same: the biological species concept (BSC) was unnecessary for practical taxonomy, neither necessary nor especially useful for evolutionary taxonomy, and neither an unique nor an heuristic concept necessary for generating hypotheses in evolutionary theory.

Ehrlich, Holm, and Parnell (1974) resurrected Ehrlich's study in the concluding, philosophical chapter of their undergraduate textbook, *The Process of Evolution.* By 1974 the debate between "evolutionary" taxonomists and pheneticists had become rather stale, but Ehrlich *et al.* did not relent on the "big" issues. If the phenetic perspective were to prevail, the BSC—with its presumption that phylogeny could be inferred at all—had to go. Despite persuasive rhetoric, it has not. It is interesting to contemplate the reasons for its persistence: mere inertia, or did the BSC really have something useful to offer?

As an evolutionist who works on butterflies and has to commit taxonomy from time to time, I found myself wondering just what, if anything, Ehrlich's 1961 survey had told us about the "species problem." It occurred to me that some kind of re-examination of his groups of genera after 20 years, with an eye to how the passage of time had affected our perceptions of species, might provide some inferences concerning the "usefulness" of the BSC, and the way we actually do use it, if we do.

My first impulse was to go through the lists, genus by genus, examining revisionary work done since 1961 to see whether ambiguous relationships had been clarified. I quickly gave up this idea. Such a genus-by-genus re-evaluation would have to be done by Ehrlich, not me, since his criteria for grouping the genera were of necessity vaguely defined. Even if I could reconstruct them, I doubt that I could interpret the changes fairly since I had disagreed in 1961 with the placement of perhaps a third of the genera. (There is also the peculiar problem that since 1961 a wave of splitting by butterfly taxonomists has so fragmented most of the genera that a newcomer to the field would be baffled by Ehrlich's lists.) But there is a more serious objection to this procedure: what would one learn from it? At the end of the exercise it might be possible to say that our wisdom regarding species increased by some quantity x, per year; one might even extrapolate to predict how long it would take to finish off the systematics of the Nearctic butterflies altogether. This is absurd, and its absurdity should become even clearer later in this paper.

## Two Case Histories

A more fruitful approach, I decided, would be to examine a couple of genera I know well, having worked on them—*Lethe* and *Pieris*. Both of them must be reclassified in the Ehrlich scheme under any reasonable man's criteria: *Lethe* has gotten more troublesome and *Pieris* (or the *Synchloe-Pontia* end of it) less so. It now seems to me that the development of my own taxonomic judgments in these genera illustrates the fact that the BSC is still very useful.

*Lethe* was listed by Ehrlich among his Group I genera—those in which "the species are quite distinct, and are considered by most workers to present no serious problems." This was perhaps a plausible judgment in

1961, but not for long. In 1966 Harry Clench, and in 1968 Ring Carde and I, perceived the possibility of sibling species concealed in the taxon *Lethe eurydice* Johansson. We all arrived at this notion in the usual way one discovers sibling species—by way of biological, not morphological differences; we observed habitat selection. Later, again in the usual way, we found morphological and color/pattern characters which supported the hypothesis that two species were involved. But these were "weak" characters hitherto unnoticed by taxonomists and which would never in themselves have been interpreted as significant at the species level by a conventional museum worker. Virtually simultaneously, C. F. dos Passos made the same discovery and published the first note on it (dos Passos, 1969). We revised his preliminary taxonomic conclusions in an exhaustive paper (Carde, Shaprio, and Clench, 1970), relying heavily on biological and behavioral data such as those reported in Shapiro and Carde (1970). It is now generally accepted that *Lethe eurydice* and *Lethe appalachia* Chermock are distinct species which are sympatric over the northeastern quarter of the United States and perhaps adjacent Canada, but also have extensive allopatric ranges. As the person most responsible for this, I argue that the significance of the habitat selection practiced by these animals in sympatry could only be made out by an observer trained in and using the BSC, whether consciously or otherwise. I also argue that the application of numerical techniques to a large unsorted collection of both species, prior to their recognition by us, would not have generated any suggestion that anything very interesting was going on.

Later the taxon *Lethe portlandia* Fabricius "fell apart" in the same way (Heitzman and dos Passos, 1974). Here the sympatry is seemingly less extensive and the level of differentiation (species, subspecies, or something inbetween) less clear; but again the discovery of morphological criteria to discriminate among the taxa was contingent on the initial discovery of biological differences in sympatry. Again, I argue, this in turn depended on the mind-set attendant on the BSC. On similar grounds, J. H. Masters has suggested yet a third sibling species may be concealed in "*portlandia.*" Ehrlich, Holm, and Parnell (1974) stated that "investigations of insects, which did not start from the premise that organisms must occur in distinct clusters, have indicated that the ease with which various groups of insects may be fragmented into distinct biological species has indeed been overestimated." Granted a bias—that species do exist in *Lethe*—I cannot see how actual reproductive isolation among natural sympatric populations (subsequently confirmed for *Lethe* by electrophoresis, Angevine and Brussard, 1979) can be interpreted as an artifact of that bias. Historically, the BSC was essential to this study, in a noncircular way.

*Lethe* in North America went, in less than a decade, from being a staid genus of three "well defined" species (*eurydice, portlandia,* and *creola*

Skinner—I would have thought the last uncomfortably close to *portlandia* to be "well defined" in the Ehrlichian sense!) to being an exciting cluster of five or six or more species arranged in two sibling-species complexes, forcing us to think about why some lineages are prone to speciate with minimal morphological differentiation. Which of Ehrlich's categories fits *Lethe* now? Probably Group 2 ("most species seem distinct, but the status of some forms is in doubt at the present time").

Ehrlich puts *Pieris* in Group 3 ("many or most species present serious problems") because of "the complete confusion regarding the status of the *protodice-occidentalis-calyce-sisymbrii-beckerii* series of forms." (It is plain today that there *is* almost complete confusion in the *napi* Linnaeus group of taxa—Bowden, 1981. The current splitters put *napi* in *Artogeia* and the above list of species variously in *Pontia, Synchloe,* or *Pontieuchloia.*) I frankly have never understood where this "complete confusion" came from though an excellent way to *become* completely confused is to read the only pre-1970 attempt to revise the group, a Master's thesis by W. P. Abbott, part of which was unfortunately published (Abbott, Dillon, and Shrode, 1960); perhaps this disaster was on Ehrlich's mind. The taxa *beckerii* Edw. and *sisymbrii* Bdv. may be removed from the muddle immediately. Both are utterly distinct from each other and from anything else in North America; in fact they are "better species" than most Pieridae and indeed most butterflies. Even Abbott would have excused them from being sunk in his morass of misused mathematics had he ever seen their larvae and pupae!

This leaves *protodice* Bdv. & LeC., *occidentalis* Reakirt, and *calyce* Edwards. Ehrlich is still confused by these in 1981 (P.R.E., *pers. comm.*). Confusion has arisen because there is great phenotypic plasticity, much of which is seasonal and mediated by photoperiodic and temperature influences during development. The control of seasonal and altitudinal phenotypes has now been worked out for a series of geographic populations (Shapiro, 1968, 1973, 1975a,b,c) and the ecological interactions of sympatric populations studied (Shapiro, 1975d). The sexual behavior of both wild animals and caged livestock supports the inferences drawn from environmental experiments, concerning the nature of species in this group. Chang (1963) attempted to justify the distinction between *protodice* and *occidentalis* morphologically. As in *Lethe*, the specific characters are "weak" and unable to stand without strong biological support. We now have that support and can say with considerable confidence that there are two biological species in North America, *protodice* and *occidentalis*; that gene flow between them is a rare, accidental event even when they are abundant in sympatry; and that the taxon *calyce* has been misused in a subspecific sense and should be sunk into infrasubspecific limbo under *occidentalis* (Shapiro, 1976).

On the other hand, study of the Alaskan population, named *nelsoni* by

Edwards, suggests that the proposal by Higgins and Riley (1970)—that *occidentalis* is conspecific with the Palaearctic taxon *callidice* Hbn.—may well be correct. (The same possibility occurred to W. H. Edwards almost a century ago; I am indebted to F. Martin Brown for bringing this non-coincidence to my attention.) Higgins and Riley similarly propose that *P. beckerii* is conspecific with the Palaearctic *P. chloridice* Hbn. This question of conspecificity of allopatric forms is a nagging one, often thrown up by those arguing against the applicability of the BSC in taxonomy (cf. Sokal and Crovello, 1970). We are saved from having to rehash the arguments here by the fact that Ehrlich expressly excluded it from his criteria in classifying the Nearctic genera by ambiguity at the species level. Based solely on the Nearctic fauna, then, I move *Pieris* from Group 3 to Group 1.

I worked on *Pieris* not to redeem it from Abbott or to clear up its taxonomy, but to unravel the history of seasonal adaptation, including polyphenism, in the group. The experimental techniques employed in this regard (reviewed by Shapiro, 1980) can provide good evidence that invasion of severe climates has been accomplished via selection of genes affecting developmental thresholds, but *only* if one assumes that the phylogenetic affinities of the populations can be known. Thus the unraveling of seasonality, and the generation of an historical model with a bearing on a variety of questions from the genetic control of physiological characters to the nature of latitudinal species-diversity gradients, cannot be separated from the unraveling of relationships which become taxonomic when the BSC is employed. Neither makes sense without the other. Obviously the potential multivoltinism/polyphenism of univolting/monophenic populations provides an additional character for numerical taxonomy, but would a pure pheneticist be able to make any biology out of it—if it ever occurred to him to do the experiment at all?

In summary, I maintain that both the increase in number of species recognized in *Lethe*, and the decrease in *Pieris*, were accomplished only because in each case the supposition was made from the start that *there were biological species in these groups*. This is not as circular as it looks. It is presumably possible to arrive at the same conclusions purely phenetically, but not unless the BSC had been used before by field and lab workers since the characters necessary to generate clusters would never have been recognized at all. Ehrlich (1961) says of phenetic classification, "Using such a system it seems obvious that any organisms sufficiently distinct to be sympatric without interbreeding will fall in distinct clusters." Perhaps, but first someone must look for them.

## Conclusion

We should be at pains to distinguish between the validity of the BSC as concept or as a mirror of Nature, and its utility in taxonomic practice. I have tried to show that the latter grows out of the former. To me Ehrlich's generic breakdown was merely a demonstration that in a group as thoroughly worked over as the Nearctic butterflies, we are bound to observe the process of transspecific evolution. Ehrlich says (1961): "There are few, if any, groups of equivalent size that are as well-known systematically as the butterflies. Vast collections of them have been amassed. . .the literature is replete with observations on their distribution and. . .their genetics and behavior. If the BSC is usable, it should be easily applicable to. . .the Nearctic butterflies." But this is equivalent, in the context of Ehrlich's argument, to saying that the BSC requires that no evolution occur. Precisely *because* the Nearctic butterflies are so well-known, we should expect them to show many more ambiguities than (say) the bat fleas of Mongolia. The fuzziness of species boundaries is not only predictable from Darwinism; it is an indispensable proof that evolution occurs. If species were well-defined all or even most of the time, neither Darwin nor we would have much reason (beyond pure cussedness) to doubt special creation. The "BSC" demolished by Ehrlich is a caricature, made to appear required to do what it cannot and never could do. Unless we are willing to read evolution out of systematics, the BSC will always be useful in forcing us to think evolutionarily. Whatever one thinks of cladistics, it has reminded many biologists of the importance of the biological species as a unit of evolution and of speciation as a (normally) irrevocable event. The species definition used by Eldredge and Cracraft (1980), though clearly tailored to cladistic specifications, shows a real phylogenetic relationship with Mayr's BSC.

Extremist positions, embraced in the name of consistency, are useful in pointing out problems which we are prone to overlook in everyday practice. As with Aleister Crowley's occult beliefs, quoted at the beginning of this paper, they cease to be entertaining or stimulating once one begins to take them too seriously. The prime virtue of the BSC, and the reason for its survival despite so many withering polemics, has been its ability to generate interesting questions of evolutionary, biogeographic, and systematic interest about real organisms in the real world. In the words of a noted taxonomist: "There seems to be little reason for taxonomists to attempt to reclassify the biosphere numerically, biochemically, or in any other way. For most naming and classifying, the techniques in use today produce special classifications which seem quite adequate" (Ehrlich, 1967).

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# Butterflies and Biospecies

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**Abstract.** A reexamination of the biological species concept confirms Ehrlich's 1961 conclusion that it had, by then, outlived its usefulness. This in no way lessens the importance of thinking in evolutionary terms when studying the biology of butterflies.

It seems appropriate, as Shapiro (1983) suggests, to reexamine the conclusions Ehrlich (1961) drew more than two decades ago about the ease of recognizing "biological species" in butterflies. One should do so in the context of what has happened in systematics during that period.

What might be called the "numerical taxonomy revolution," begun by Michener and Sokal's (1957) work with bees and Sneath's (1957a, b) studies of bacteria, as Shapiro indicates, has run its course. It caused a fundamental reevaluation of the intellectual underpinnings of taxonomy, changed forever how detailed (but not routine) taxonomic investigations are done, and led to a reexamination of the biological species concept (BSC). Ehrlich's original conclusions—that the concept was misleading and not very useful—were basically confirmed by Sokal and Crovello's (1970) more detailed examination. Since then, nothing has appeared in the general literature to give any reason for changing those conclusions.

The difficulty with the biological species as a taxonomic category is that, where it might be useful, it is impossible to apply. Biological species were defined by Ernst Mayr (1940) as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups". Under that definition the test of whether two phenetically similar forms are part of the same species or of different species is what happens when they occur together *in nature*. Where the forms are sympatric and synchronic, a clear decision *may* be made impossible by partial interbreeding (or, more often, by practical difficulties in determining whether there is interbreeding at all). But insurmountable problems arise when considering allopatric populations, since there is no way to predict what would happen if the two similar forms later became sympatric (Ehrlich, 1961). And yet *application* of the BSC requires prediction of the potential for interbreeding.

To give a simple example, *Euphydryas editha* populations in the San Francisco Bay area (subspecies *bayensis*) have been isolated from *E. editha* in Colorado (*gunnisonensis*) for at least 7000 generations (Ehrlich and White, 1980). It has been that long since suitable habitat was more or less continuous across the now-arid intermountain region. The two sets of populations feed on different foodplants, adult flights are completely allochronic, and they are genetically and phenetically at least somewhat differentiated (Brown, 1970; Ehrlich et al., 1975; Ehrlich and White, 1980; Holdren and Ehrlich, 1982).

While trying to elucidate patterns of speciation in *Euphydryas*, our research group would like to evaluate behavioral and genetic incompatibilities between these sets of populations, but so far the difference in their phenology has not even permitted us to obtain adults from both populations simultaneously in the laboratory. If we did, and if we could assume that laboratory behavior was the same as behavior in nature (we could not), the results would still not tell us with assurance what would occur if the two became sympatric in nature.

Suppose it became possible for *Euphydryas* once again to occupy the intermountain regions and the agricultural Central Valley of California. If that happened, a completely unpredictable set of ecological and selective events would occur *before* significant opportunity for interbreeding could exist. Populations of *Euphydryas editha* and a wide diversity of potential host plants would reinvade the lowlands from many refugia. The silliness of trying to imagine such a "test" of whether *bayensis* and *gunnisonensis* were conspecific is clear. It would not, in all likelihood, even be possible to identify two groups of *editha*-like butterflies as *bayensis* and *gunnisonensis* descendants.

The basic point is that the California and Colorado *E. editha* are classified in the same species on phenetic grounds—because they look alike, behave alike in many respects, feed on chemically similar foodplants, have similar allozyme genetics, and so forth. Should laboratory tests show some degree of genetic incompatibility—which seems not unlikely on the basis of preliminary intercrossing of other *Euphydryas* populations (Odendaal and Ehrlich, unpublished)—we probably would still continue to consider them conspecific.

Only if it were certain that successful interbreeding is now impossible *and* that compatibility could not be restored by selection during a long period of migration leading to sympatry would we elevate *E. e. gunnisonensis* to specific status. The latter is especially important, since incompatibility today appears largely a matter of asynchrony, which might well evolve back toward synchrony. Taxonomists have always agreed that sexually reproducing populations between which interbreeding is obviously impossible belong to separate species—to our knowledge no one has suggested lumping *E. editha* and *Felis tigris* even though no tests of potential interbreeding have been attempted.

The judgment of impossibility of interbreeding of certain *Euphydryas* populations can be made strictly on phenetic grounds—for color pattern, genital morphology, mating behavior in the laboratory, chromosome behavior in hybrids, fertility in crosses, viability of hybrid offspring fed different larval hosts, and so on, are all aspects of the phenotype. For example, the Colorado *E. editha* can reasonably be considered not to be conspecific with *E. phaeton*. Phenetic analysis, including the behavior of individuals toward one another in the laboratory and allozyme analysis, shows them to fall into very distinct clusters. But this does not involve the application of the BSC—*E. editha* and *E. phaeton* were recognized as distinct *kinds* of organisms long before anyone thought about the BSC.

In short, where two kinds are sympatric and noninterbreeding, or allopatric and very distinct, the BSC adds nothing. Where they are allopatric and not very distinct, it provides no tool—even in theory—for deciding where the species boundaries should be drawn. It is thus useless in practice.

We are, however, in agreement with many points of Shapiro's paper. It is very important for systematists to think evolutionarily, for they are classifying products of evolution, and the patterns those products show in nature throw light on the process. For example, the pattern to be expected under the "punctuated equilibrium" hypothesis (Gould and Eldredge, 1977; Stanley, 1979) would, in most time periods, be quite different from that anticipated under a Darwinian—that is, a more gradual—regime (Lande, 1980). Work now going on in our group indicates a spectrum of levels of differentiation in *Euphydryas*, the kind of pattern one would expect if speciation were constant and gradual. It is our impression that this sort of pattern is common in butterflies, and that the group as a whole shows no sign of speciational stasis.

A reexamination of Ehrlich's 1961 categorization of butterfly genera according to the distinctness of the species contained in them is instructive. If the world were mostly made up of "good species" in the stasis stage of the punctuated equilibrium model of speciation, one would expect to find few genera in which there was any debate about how many species there were and which populations belonged to which species. This is especially true in a group as continually studied as the butterflies—although first-rate biologically oriented studies such as those of Shapiro on *Pieris* make up a depressingly small proportion of the work.

Most of the genera in the 1961 list would remain in the same place today, as a few examples will show. There are still no difficulties with recognizing the Nearctic species of *Nymphalis* as distinct, and still no resolution of the relationship of several of those with European populations. For instance, what would happen if the North American *Nymphalis milberti, N. californica,* and *N. vau-album j-album* became naturally sympatric with the Palearctic *N. urticae, N. polychloros,* and *N. vau-album vau-album* is unknown and unknowable. The current nomenclature simply reflects the guesswork of taxonomists who may think they are studying biological species.

The problems with *Papilio* persist, with opinions widely varying on relationships within the *machaon* group. Indeed, a new "species" (*P. joanae*) has been added to the mess since Ehrlich wrote. The relationship of *Papilio glaucus* and *P. rutulus* remains in doubt—some believing they are "good species" and others (J. Scott, pers. comm.) that they are conspecific. *Speyeria, Boloria, Oeneis, Cercyonis, Coenonympha, Chlosyne,* and so on remain confused, with much rearranging but no appearance of neat clusters.

Results from groups that have been particularly well studied since 1961, such as *Phyciodes* and *Euphydryas* show complexity, not neat biospecies. Populations of *Phyciodes tharos*, for instance, exhibit genetic incompatibility (egg infertility) that gradually increases with distance (Oliver, 1972). Incompatibility between *P. tharos* and *P. campestris* differs only quantitatively from that within *P. tharos* (Oliver, 1978), while crosses between *P. tharos* and *P. batesii* show not only lowered egg fertility but developmental abnormalities as well (Oliver, 1979).

In *Euphydryas* the relationship between closely-related *E. chalcedona* and *E. anicia*, considered conspecific by Scott (1978), is particularly complex. For example, in the Pequop Mountains of northeastern Nevada, black *E. chalcedona nevadensis*, which oviposits on *Symphoricarpos*, flies sympatrically and synchronously, with no sign of interbreeding, with red *E. anicia wheeleri* which oviposits on *Castilleja chromosa*. Black *E. chalcedona olancha* on the east slope of the Sierra Nevada intergrades in genitalic characters and wing color with red *E. anicia wheeleri* on the west edge of the Great Basin. Both oviposit on *C. chromosa*.

The situation in *Lethe* has, as Shapiro points out, become more complex since 1961—although we cannot see any validity to his claim that the biological species concept (as opposed to recognizing that habitat selection is an important aspect of the phenotype) had anything to do with the recognition of the sibling species. No one disputes (or has disputed) that sympatric, synchronic populations that do not interbreed should be considered to belong to separate species (for simplicity, we will ignore the infrequent problem of "circles of races" here).

What Ehrlich predicted was that in cases of sibling species careful numerical phenetic analysis would produce discrete clusters. We know of no test subsequent to Ehrlich's that has been made of that claim, but since Carde et al. (1970), using purely phenetic data, established the specific distinctness of *Lethe appalachia*, Ehrlich's claim still appears to be valid.

In fact *eurydice* and *appalachia* were considered morphologically distinct more than 35 years ago (Chermock, 1947). The subspecific designation of *appalachia*, however, was based on inadequate information. With a type series of only 33 individuals from several states, Chermock mistakenly thought there was an "overlap of diagnostic features." He was wrong; Carde et al. (1970), with many more specimens, found in a survey of 20 phenetic characters that they "differ subtly but consistently."

Shapiro's studies have certainly extended our understanding of *Pieris* since Ehrlich's original paper. As in *Lethe*, differences in phenotypically similar *Pieris occidentalis* and *P. protodice* were noted early, then documented and specific status assigned (Chang, 1963), well before a lack of interbreeding was described in a zone of sympatry (Shapiro, 1975). Shapiro recently admitted (pers. comm.) that he was puzzled about the status of some forms of the *P. napi* complex in North America. The more vexing question of whether Nearctic *P. occidentalis* should be considered conspecific with Palearctic *P. callidice* remains unresolved. Shapiro's (1980) finding of substantial genetic incompatibility between geographically distant Alaskan and French populations is not surprising in view of Oliver's (1972) findings with *P. tharos* and those of our group (Odendaal and Ehrlich, unpublished) on incompatibility within species of *Euphydryas.*

Shapiro's work shows how thinking evolutionarily can enrich our understanding of taxonomic complexes. Thinking evolutionarily, however, is not the same as assuming that butterflies can be divided into biological species, or that "species" would represent the same things in different taxonomic groups, including different groups of butterflies. For example, the old idea that all species in sexually reproducing organisms are evolutionary units bound together by gene flow appear to be incorrect (Ehrlich and Raven, 1969).

We do disagree completely with one of Shapiro's statements—that is, that there is a connection between the biological species concept and the "presumption that phylogeny could be inferred at all." Note that, in Mayr's quoted definition, there is no phylogenetic or historical element; in fact it could be adopted by a creationist! Basically, however, we think there is very little disagreement between our position and that of Shapiro—mostly a terminological difference. We all agree that careful breeding experiments, ecological studies, and laboratory investigations of development under different environmental regimes are most useful in understanding the evolution of butterflies and can lead to enormous improvements in taxonomy around the species level. Shapiro believes that this is applying the BSC; we contend it is simply applying phenetics.

We enthusiastically endorse Shapiro's observation that Darwinism predicts the "fuzziness of species boundaries"—indeed we would go further. Our working hypothesis is that Darwinism predicts a continuum of differentiation from "same population" to "distinctly different species."

We think that approaching nature with the notion that the question "is it a good biological species?" can normally be answered yes or no has biased the view of organic diversity *away from a Darwinian (gradualist) interpretation*!

In summary, we agree with Shapiro that studying the genetic/interbreeding relationships of populations is a useful exercise for systematists, and may often produce information that is useful in making taxonomic decisions. We also believe that the biological species concept once played a very important role in focusing thinking about processes of speciation, and that Mayr's basic view that speciation is primarily allopatric is correct. But, because of the impossibility of defining actual and, especially, *potential* interbreeding, taxonomists do not and cannot use the biological species concept to determine what are or are not "good species"—even if they imagine they are so doing. And in so imagining, they contribute to a biased and basically anti-Darwinian view of the patterns of differentiation found in nature.

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# The Biological Species Concept and the Aims of Taxonomy

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**Abstract.** The aims of taxonomy are considered twofold: to describe the diversity of the living world, and to understand the processes that have led to this diversity. A natural classification expressing phylogenetic relationships among taxa is a means to present the results of a taxonomic study in a condensed form. The biological species concept is considered indispensable for a natural classification as it gives the unit of classification, the species, a natural basis.

> "The species has a different significance to
> the systematist and to the student of evolution."
>
> Mayr (1942: 113)

When, in the fifties, electronic data-processing techniques assumed enormous proportions, the expectations of some biologists soared high. Taxonomy in particular, with its wealth of data to be processed into a classification, seemed particularly fit to apply the new technique to. As is often the case when a new technique or a new idea has been developed, some people saw it as the final answer to many questions. Ehrlich (1961a) went so far as to predict the impending death of traditional taxonomy. The following quotations from his predictions concerning the situation in 1970 are relevant here: "Relationships will be presented in condensed form, either as a matrix of coefficients measuring similarity, or as a dendrogram expressing the structure of such a matrix", and "Emphasis will have shifted away strongly from the naming of different kinds of organisms towards the description of the interactions among them." In such a prophesy there is hardly need of any species concept. It is therefore remarkable that Ehrlich (1961b) considered the question of whether the biological species concept (BSC) is a useful taxonomic tool, and not the species concept in general. I think his rejection of the BSC follows from his concept of taxonomy. Ehrlich, however, used quite a different, and in my opinion incorrect argument to arrive at his negative conclusion. Shapiro (1982) already demonstrated the inadequacy of Ehrlich's argument, but he did not deal with the BSC in relation to the aims of taxonomy either. As it is clear that the usefulness of any species concept in taxonomy depends on one's concept of taxonomy, I would like to discuss this concept first and then to consider if and how the BSC fits into this context.

## Taxonomy

I fully agree with Ehrlich (1961a) when he states that mere collecting and describing new species does not further our understanding of the world of life. It is also true that many taxonomists, particularly entomologists, do little else than to collect and describe new species. As much of this work is done by amateurs, who have neither the time nor training to go deeply into the theoretical background of taxonomy, I think it unfair to suggest that such efforts represent some kind of mental abnormality. There are also many professional entomologists who are not too occupied by theoretical considerations, but they are usually specialists of groups which are yet poorly known. It is easy to say that one should use "judicious sampling in our efforts to understand the universe", but what is judicious when your best guess is that only 10 or 20% of the species of your chosen group are known? Ehrlich's remarks remind me of a political debate in The Netherlands some years ago on a proposed huge land reclamation project in the Wadden Sea. This sea is a vast tidal area that stretches over some 150 km in the northern part of the country. As it is very rich in animal life and of utmost importance to migrating birds, biologists crowded together to oppose the plans, thereby stressing the importance of the area for the study of the diversity of life. One of the politicians then remarked, that since they did not yet understand life in the Wadden Sea, the area was apparently too big for the biologists to finish the job. Therefore, it would be a good idea to reclaim most of it and to reserve a small part for the biologists, small enough to offer them the opportunity to complete their studies. This man clearly did not understand the extent of the problem. I am afraid Ehrlich did not understand it either. Although collecting and describing new species do not in themselves further our understanding of the world of life, they provide materials for framing and testing hypotheses, and that is the way science proceeds. We simply cannot collect and describe enough, certainly in view of the alarming destruction of rich natural habitats, not to "finish the job" as suggested by Ehrlich, but to find new materials and additional data for a better understanding of life. Mound (1983) may be correct in supposing that the tropics are too rich in arthropods to ever been known adequately because of lack of funds and time. Such opinion does not imply, however, that collecting and describing is senseless, it only makes clear that it is a castle in the air to suppose that the job could ever be finished.

In my opinion Ehrlich demonstrated a too restricted view of taxonomy, which he more or less synonymized with classification. He also demonstrated a restricted view of evolutionary problems when he said: "Large general collections will retain value as records of the diversity of life, but their value in scientific research, already much decreased, will become nil. It is already apparent that the worker on evolutionary problems must, in most cases, do his own sampling, suited to his own special problem." Although this view may be true for Ehrlich's evolutionary problems at the population level, it is certainly not true for evolutionary problems at higher taxonomic levels. For instance, I faced the problem of the evolution of secondary sexual characters in the genus *Celaenorrhinus* (Hesperiidae) (de Jong, 1982). It think this is a legal evolutionary problem, which I attacked by studying material from large general collections. Without such collections, it would not even have occurred to me that there was a problem.

It is not surprising that in his restricted view of taxonomy and evolutionary problems, Ehrlich embraces the computer as the machine that can relieve us of much tedious work. If one is not interested in evolution above the population level, why should one try to arrive at a classification that is anything more than typological? Whatever the number of unweighted characters put into the computer, the output is no less typological than in the way since Linnean times. By varying the characters we feed into the computer, we get varying classifications. This conclusion is not surprising, and common sense seems as good a way to reach this conclusion as a computer. I fully agree with Ehrlich & Ehrlich (1967) when they state that all classifications thought of as being general, and based on overall similarity, are in reality special classifications, because they are always based on a limited and selected set of characters. As a typological classification is dependant on the characters chosen, typological classifications based on different sets of characters are all equally true. A classification of the various kinds of apples, for instance, based on the colour of the ripe fruit, is as good as one based on the thickness of the skin or the number of pips. The choice of the classification depends on its practical value. The same applies to a typological classification of the butterflies. The differences in the classifications listed in Fig. 1, for instance, are possibly due to differences in practical value, as the authors had a different scope in their work (the data clearly show the widespread tendency to splitting when the geographic or taxonomic scope narrows). To me, these classifications all have the same practical value: an easy reference system, where the place of a classified unit is an indication of what this unit looks like with respect to the characters on which the classification is based. Therefore, I don't see the use of constructing new typological classifications, or as Ehrlich & Ehrlich (1967: 316) have put it: "There seems to be little reason for taxonomists to attempt to reclassify the biosphere numerically, biochemically, or in any other way."

If we, as Ehrlich apparently does, consider the drawing up of a typological classification the aim of taxonomy, taxonomy becomes only a means to register characters, and not a scientific discipline. The resulting

| Kristensen 1976 World | | Ehrlich 1958 World | | Howe 1975 N. America | | Higgins 1975 Europe | |
|---|---|---|---|---|---|---|---|
| Papilionoidea | Papilionidae | Papilionoidea | Papilionidae | Papilionoidea | Papilionidae | Papilionoidea | Papilionidae |
| | Pieridae | | Pieridae | | Pieridae | | Pieridae |
| | Lycaenidae | | Lycaenidae | | Lycaenidae | Lycaenoidea | Lycaenidae |
| | | | | | Liphyridae | | |
| | | | | | Riodinidae | | Riodinidae |
| | Nymphalidae | | Libytheidae | | Libytheidae | Nymphaloidea | Libytheidae |
| | | | Nymphalidae | | Heliconiidae | | |
| | | | | | Nymphalidae | | Nymphalidae |
| | | | | | Apaturidae | | |
| | | | | | Satyridae | | Satyridae |
| | | | | | Ithomiidae | | |
| | | | | | Danaidae | | Danaidae |
| | Hesperiidae | Hesperioidea | | Hesperioidea | Megathymidae | Hesperioidea | |
| | | | | | Hesperiidae | | Hesperiidae |

Fig. 1. Phenetic classifications of butterflies (Ehrlich, 1958; Howe, 1975; Higgins, 1975) may differ considerably, but all are equally valid. The only phylogenetic classification of the butterflies at family-level is the one by Kristensen (1976). See text for further comments.

classification is a classification of characters, not of organisms. If we, contrarily, start from the notion that evolution has occurred and is still occurring, and are interested in the question of how and why evolution has occurred in the group under study, the classification of characters is only a first step in answering the question. If we pose the right questions, nature will give the right answers. It is currently considered that such questions should be posed in the form of testable and rejectable hypotheses (e.g., Popper, 1962). In this way taxonomy can develop into a scientific discipline. To grasp the problems involved, a first ordering of the characters, a typological classification, is needed. There is, however, no need or excuse to stop here. Otherwise we could as well keep collecting stamps or cigar bands. Butterflies, in which so many characters have been studied, and which are so well known biogeographically, seem to be an ideal group to study from the evolutionary point of view. Although many evolutionary problems, especially at the population level, are studied with the help of butterflies, the phylogeny of butterflies is still largely unexplored. The only paper dealing with the phylogeny of the butterflies, in the form of testable hypotheses, is that by Kristensen (1976), who was concerned only with the phylogenetic relationships of the families. Remarks in the literature as "not surprisingly, the family Hesperiidae presents the most primitive radial arrangement within the Papilionoidea" (Brock, 1971: 62) have little to do with phylogenetic research, since the remark is based on circular reasoning. Accordingly the Hesperiidae are first considered primitive because of their radial arrangement (thus, it is correct to say that the conclusion is not surprising).

The peculiar situation of a group of organisms so well-known biologically and yet so badly known phylogenetically is partly due to the view of some students that it is impossible to reconstruct the phylogeny of the butterflies. At least, I taste this view from the words of Ehrlich & Ehrlich (1967: 315): "The impossibility of achieving a *general* phenetic classification does not call for a return to so-called phylogenetic classification. Any phylogenetic classification would be based on similarity judgments, and thus attempts to construct such a phylogenetic classification would be subject to the same restraints as constructing a phenetic classification based on overall similarity." I think such a view does not entirely do justice to current methods of phylogenetic research. Suppose there are three species, A, B and C, with characters a, b, x and y, distributed as in Fig. 2, where their phylogenetic relationship is also shown. Phenetically we could classify A with B on the basis of common possession of character a, or B with C on the basis of common possession of character y. Both classifications are equally correct from the phenetic point of view. If the classification, however, reflects the phylogeny of the three species, there is

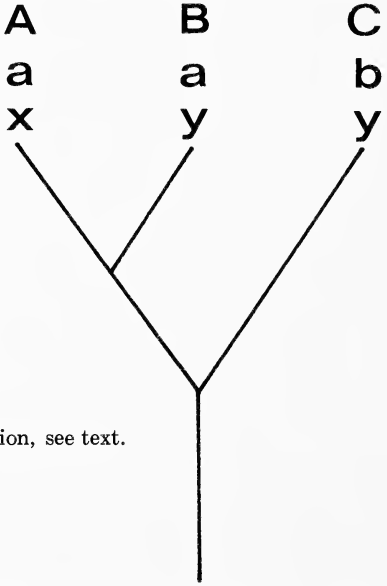

Fig. 2. For explanation, see text.

only one correct classification, namely that which reflects the true course of history. We try to find this course by comparing characters within the group as well as outside it (see, e.g., de Jong, 1980). In this manner we arrive at a hypothesis of the phylogeny, which may be rejected by subsequent data. The aim of the phylogenetic study is to reconstruct history and not to construct a classification. Nevertheless, a phylogenetic classification is the logical outcome of the study and presents the conclusions in a condensed form.

I cannot, therefore, agree with the view that Clench (1975: 46) expressed in the following lines: "Families have shared the same "splitting" problems as genera. Even today, for instance, some authors use Nymphalidae for the butterflies that other authors would divide among the Satyridae, Morphidae, Ithomiidae, Danaidae, Heliconiidae, Apaturidae, and Nymphalidae (strictly interpreted). There is no objective way to decide the merits of these opposing views, but time is probably on the side of the splitters." This view is undoubtedly true for a phenetic classification, but in a phylogenetic classification there is not simply a subjective choice between one big family and many small ones. The requirement of a phylogenetic classification is that the taxa recognized are monophyletic. If there is evidence in the above sample that the Nymphalidae *sensu lato* are monophyletic, but the Nymphalidae *sensu stricto* are paraphyletic, the choice is not subjective (i.e., depending on personal idiosyncrasy or individual point of view), even when the evidence later would prove to be incorrect. In a typological or phenetic classification no such requirement exists, no standard to test the correctness of the choice, and thus the choice remains subjective; any choice is as good as any other. This is a fundamental difference.

A phylogenetic classification need not differ much from a phenetic one. However, the statement that a phenetic classification is phylogenetic, to the extent it reflects the phylogeny (Colless, 1970), is senseless, since we only know the extent to which it reflects phylogeny if the phylogeny is known. In that case, why should we maintain the phenetic classification? The bearing of the kind of classification on biogeographical problems may be illustrated by the following example. Evans' (1951) classification of the Hesperiidae is phenetic. Evans concluded that the strictly New World subfamily Pyrrhopyginae and the strictly Old World subfamily Coeliadinae are two branches from the same ancestor split by the drifting apart of South America and Africa (see the present distribution of these subfamilies in Fig. 3). A closer study, however, reveals that there is no argument, except superficial similarity, to support the idea that the two subfamilies are sister groups, having originated from the same ancestor which did not give rise to other taxa. Hence, the assumption of continental drift as the key factor in the origin of these subfamilies is fully unsupported.

Similarly, the paper by Shields & Dvorak (1979) on butterfly distribution

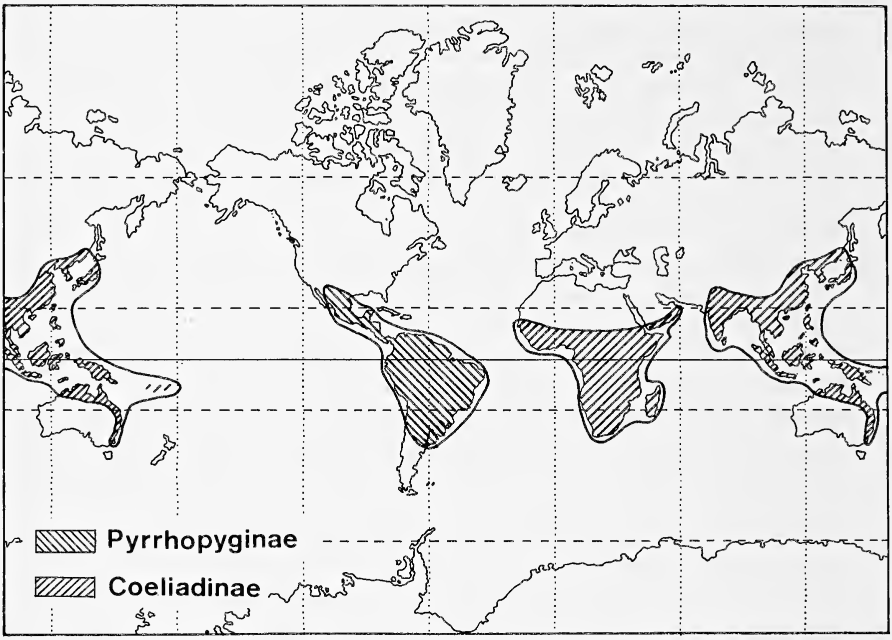

Fig. 3. Vicarious distribution of two subfamilies of Hesperiidae.

and continental drift, shows the inadequacy of phenetic classification for biogeographical studies. It is such work, with its unwarranted conclusions, that has brought taxonomy and biogeography into discredit with students of other biological disciplines. Let me cite just one example. It is stated that "Pseudopontiinae is probably derived from a moth". The "evidence" is that "In this peculiar venation it approaches such moth families as Psychidae, Chalcosiidae, Zygaenidae (*Gynautocera, Chalcosia*) (Poulton, 1922; Kirby, 1897), and Lasiocampidae (*Porela*). It also resembles some of the rounder-winged genera of Lymantridae (e.g., *Pantana*), and certain Lymantridae (*Cozistra*) and Geometridae (*Leucula*) in appearance (Kirby, 1897)." I think the best possible conclusion would be that the peculiar venation of *Pseudopontia* does not give a clue to its ancestry, unless it can be shown that the similarities are based on synapomorphy. Since there are reasons to suppose that the similarities are due to convergence (too complex an issue to deeply explore here), there is no support for the conclusion of Shields & Dvorak. Unfortunately, lepidoptera literature is full of such unsupported statements.

In summary, it is my view that taxonomy should not only aim at description, but also at an *explanation* of the diversity of life. The resulting natural classification is a way to present the conclusions in condensed form.

## The Biological Species Concept

The lengthy exposition in the foregoing chapter, which is actually a plea for a more scientific approach to taxonomy, may seem to have little to do with the BSC, but in my opinion is crucial. In Ehrlich's concept of taxonomy there is no need for the BSC, and his rejection is quite logical. In a broader, and in my opinion more scientific, concept of taxonomy, the BSC is indispensable. If we want the classification to reflect natural relations, then the unit of classification, the species, should also be "natural". This means that it is not important or even interesting as to how *we* can distinguish the species, but how the *species themselves* do it. The fact that there is no unequivocal natural test of conspecificity (or lack of same) for cases of allopatric forms cannot detract from this principle. The same applies to the fact that the criterium of the BSC, reproductive isolation, is not always complete and can occur in varying degrees. Contrary to what is apparently thought by Ehrlich, the BSC was not constructed to facilitate species recognition, but to make the species a natural unit.

If one wants to test the usefulness of a concept, the most obvious way seems to be to apply the concept and see what happens. Ehrlich (1961b) chose another direction. He investigated the classification of the North American Papilionoidea, which at that time was largely phenetic, and observed that "the prevalence of the clearly defined species is a myth." The only conclusion one can reasonably draw from his observation is that our knowledge is inadequate. To condemn the BSC for lack of knowledge, as Ehrlich did, is absurd, as long as one has not proved that indistinctnesses are due to the application of the BSC. Shapiro (1982) did apply the BSC to the classification of some Nearctic butterflies and showed that the BSC can considerably help clear up situations which are confusing to pheneticists (genus *Pieris*), and also can refine the description of seemingly clear-cut situations (genus *Lethe*, but see also below). These examples do not make the BSC a useful tool in Ehrlich's concept of taxonomy. They demonstrate that Ehrlich's concept of taxonomy is not useful in a study of the diversity of life.

The "biological species concept" is a little confusing as the term suggests that life history data form the basis of species recognition. Some authors (e.g., Clark & Dickson, 1971, in their remarks on the specific distinctness of *Lycaena orus* and *L. clarki*) seem to think that life history data are conclusive in separating species. Shapiro's remarks on the genus *Lethe* also do not demonstrate the usefulness of the BSC in itself, but the insufficiency of a purely morphological species concept. In the BSC, however, the crucial issue is reproductive isolation. Generally reproductive isolation cannot be directly observed. To do so would be practically impossible as proof would require direct observation that successful pairing between specimens of different species never occurs.

The existence of isolation, and thus the absence of gene flow, is concluded from observed differences in characters. Whether these characters are morphological, behavioral, ecological, biochemical, or whatever, is not important. Thus, the observation by Larsen (1982) on the occurrence of geographically defined differences in chromosome numbers in the Old World skipper *Gegenes pumilio* may indicate that two species are involved, even though no morphological or other differences can be found. Similarly, the difference in enzymes in South European populations of *Pontia daplidice* (Pieridae) observed by Geiger & Scholl (1982) could mirror reproductive isolation. Museum taxonomists (I know what I am talking about for I am one myself), committed as they are to the study of morphological characters, tend to overemphasize the importance of morphological characters. However, when they apply the BSC there is no objective reason why the morphologically distinct species *Danaus chrysippus* and *D. gilippus* should be "better species"* than the cytologically different forms of *Gegenes pumilio*. There is a strong tendency among lepidopterists not only to apply a morphological species concept, but to restrict it mainly or entirely to the genitalia. Niculescu (1977), for instance, has strongly stressed that a species definition should be based on genitalia. Apart from being an example of circular reasoning (Niculescu first distinguished the species on the basis of genitalic differences, and then concluded that all species did have different genitalia), this restricted morphological species concept has a drawback in those instances where the genitalia vary geographically, a kind of variation that is not very exceptional in Hesperiidae (de Jong, 1978). The latter observation does not alter the fact that genitalia are of utmost diagnostic value. In a biologically oriented taxonomy, however, genitalia are not qualitatively better than any other character which indicates that reproductive isolation exists.

As phenetic differences are usually the result of, or at least maintained by, reproductive isolation, it is not surprising that the application of the BSC does not need to have much effect on a phenetic classification at the species level. It is in borderline cases where the BSC is helpful to understand situations. I stress again, that the aim of taxonomy should include an understanding of present diversity, not a simple classification of it. In cases where two sympatric populations are not completely isolated reproductively, their relationship can be expressed numerically by, for instance, the percentages of hybridization at different localities. In my opinion hybrid frequencies would provide more information about the degree of isolation than any diagram or matrix of coefficients based on

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*The term "good species" seems to be remarkably persistent in literature, suggesting that there are also "bad species". This is absurd, of course. A population that is not specifically distinct from other populations (is not reproductively isolated), is not a bad species, but no species at all. The adjectives "good" and "bad" refer to the taxonomist, not to the species.

overall similarity. Even so, such data would be of little practical value for general use, e.g., in an identification guide or to express relationships. The point may be illustrated by the example of the common Palaearctic skipper *Pyrgus malvae* and relatives (summarized by Guillaumin & Descimon, 1976). In Central France *P. malvae* meets *P. malvoides*, which is externally very similar to *P. malvae*, but has quite distinct male and female genitalia. In France *P. malvae* is always univoltine, *P. malvoides* is bivoltine except at higher elevations. Where *P. malvae* meets univoltine *P. malvoides*, hybridization occurs at a high frequency: up to about 80% of the males were found to have intermediate genitalia. Where *P. malvae* meets bivoltine *P. malvoides* hybridization is, understandably, rare. To express this complex relationship in the most concise form, for instance by a map and a diagram expressing the degree of hybridization at different localities, would take at least one page. For an evolutionary study at the population level this may be too condensed, for any other use it is much too detailed. The observation that *P. malvae* and *P. malvoides* can still hybridize in nature is sufficiently clear from the use of the category "superspecies" for *P. malvae* and *P. malvoides* together (they are actually part of a still larger complex), or of the category "semispecies" (or "quasispecies") for both *P. malvae* and *P. malvoides*. These categories are dependant on the application of the BSC; without the BSC the categories are meaningless.

## Conclusion

The aims of taxonomy are considered to be twofold: to describe the diversity of life, and to understand the processes that have led to this diversity. The describing phase leads to a phenetic classification. When further study has elucidated the evolution of a group of organisms, the relevant data can be incorporated into the classification to make it "natural". The natural classification is not the aim of taxonomy, but a way to present the results of a taxonomic study in a condensed form. To be natural a classification should be based on a natural unit, a group of organisms that is naturally defined and can be detected as such. The only group of organisms that comes into consideration, is the group that is reproductively isolated from other groups. Such groups are called biological species. The biological species concept is, therefore, considered an integral part of taxonomy. Difficulties in its application reflect interesting evolutionary situations. The BSC is thus useful in detecting such situations.

The idea that historical events (in this case speciation) cannot be reconstructed from a study of their products (species) is considered unjustified. The methods in use today to detect phylogenetic relationships comply with the requirements of a scientific study as currently conceived. There is, therefore, no excuse to content oneself with a numerical classification, which is only a description of the diversity that in itself does not further our understanding of the living world. Thus, the statement by Ehrlich (1961b: 175): "Relationships at the lower levels of the taxonomic hierarchy should be expressed numerically, in essentially the same way as relationships of higher categories are now expressed", is rejected.

In the 20 years passed since Ehrlich published his predictions on taxonomy in general, and the BSC in particular, few of these predictions have come true. The BSC is probably more widely applied to the classification of the butterflies now than 20 years ago. It may be noted that although a better understanding of the evolution of the butterflies has not yet resulted, at least a start has been made. Ehrlich's remark that "An afternoon of rigorous field observation will usually produce more information of evolutionary value than weeks spent studying preserved material", mirrors the depreciation of the population ecologist for taxonomic work rather than an understanding of the aims of taxonomy.

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# Chromosomes of Seven Species of Indian Sphingid Moths

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**Abstract.** Chromosome cytology of seven species of sphingid moths have revealed the haploid chromosome number as n=29 in each of *Acherontia styx, Cephonodes hylas, Deilephila nerii, Macroglossum bombylans, Macroglossum gyrans* and *Theretra oldenlandiae* and n=28 in *Rhyncolaba acteus*. Peculiar lagging anaphasic movement of two of the homologues of a bivalent (possibly the XX sex-chromosome pair) during their poleward separation has been observed in three out of the seven species examined.

## Introduction

Although intense investigations on the chromosome cytology of Lepidoptera have been carried out in different parts of the world, work in India is almost negligible (Gupta, 1964; Saitoh and Abe, 1969, 1970a, 1970b; Rishi, 1973; Nayak, 1975). The present communication deals with karyological study of the male meiotic cycle of seven species of moths belonging to family Sphingidae. Five* are new to cytology. This information may be of great help in providing additional information for an understanding of cytotaxonomic situation of the group.

## Material and Methods

Larvae of seven species of sphingid moths were collected from their respective host plants (Table 1) and were reared in cages. The fifth instar larvae and early pupae were found suitable for chromosomal investigation. Testes were dissected out and fixed overnight in 1:3 acetic alcohol. Permanent squash and smear preparations of the material were made following the technique of Smith (1943) and slides were stained in Heidenhains Iron Haematoxylin. Slides were examined under a Meopta Binocular Research Microscope and good metaphase stages were drawn using a 100X oil immersion objective and 15X occular with a camera lucida. Some of the stages were photographed.

TABLE 1

| Name of Species | Host plant | 2n | n |
|---|---|---|---|
| *Acherontia styx* Westw. | *Sesamum indicum* | 58 | 29 |
| *Cephonodes hylas* Linn. | *Gardenia* sp. | 58 | 29 |
| *Deilephila (Daphnis) nerii* Linn. | *Oleand* sp. | 58 | 29 |
| *Macroglossum bombylans* Bois. | *Paedera* sp. | 58 | 29 |
| *Macroglossum gyrans* Walk. | Unidentified | 58 | 29 |
| *Rhyncolaba acteus* Cram. | *Impatins* sp. | 56 | 28 |
| *Theretra oldenlandiae* Fabr. | *Colocasia antiquorum* | 58 | 29 |

## Observations

### *Acherontia styx**

The diploid number (2n) at spermatogonial mitosis consisted of 58 small, spherical and dot-like chromosomes in a circular arrangement. In both size and morphology, the chromosomes were almost identical. Sex chromosomes, if any, remained unidentifiable. The meiotic prophase chromosomes in zygotene and pachytene stages were elongated and thread-like paired bodies, almost half that of the number of spermatogonial metapase chromosomes. Their exact number, however, was not countable. The pachytene bivalents were faintly stained and appeared to be shorter and thicker, providing evidence of a lengthwise pairing of homologous chromosomes. However, the exact nature and position of chiasmata upon them was not clear. The early diplotene appeared indiscrete. The chromosomes became more and more condensed and stainable as they passed through diakinesis to metaphase I. The mid and late diakinetic bivalents had an uneven distribution in the nucleus and presented various chiasma bearing shapes like V, dumbbell, cross, rod and ring suggesting the positive occurrence of chiasmata. The metaphase I bivalents were at maximum state of condensation and were oval in shape. In most of the diakinetic and metaphase I plates, 29 bivalents were encountered. Deviation from this number was also noticed in many metaphase I cells. Some of the elements appeared relatively smaller and thus might be univalents formed by early resolution of some bivalents. A peculiar anaphase behaviour was recorded in certain anaphase I plates where two of the separating elements, probably the homologues of a bivalent, still occupied a position in the equatorial plate during their poleward movement when all others had reached the poles. The lagging anaphasic movement is characteristic of sex-chromosomes and possibly this pair constituted the XX-sex chromosome pair. Metaphase II presented 29 dot shaped univalent chromosomes which is in conformity with the haploid chromosome number of the species (Figs. 1 to 4).

*Cephonodes hylas**

2n=58. Polar as well as equatorial views of metaphase I stages showed clearly 29 bivalents. The chromosomes were oval in polar view, but almost dumbbell-shaped with a notch across the middle in equatorial view. Early separation of a bivalent into two distinct elements were observed in 14 out of 171 nuclei examined. Metaphase II showed 29 small univalent chromosomes, establishing the haploid number n=29 (Figs. 5 to 7).

*Deilephila nerii**

2n=58. Two of the chromosomes appeared to be positively heteropycnotic. Metaphase I cells showed 29 bivalents, one of which was more deeply stained. In some cells there was an early resolution of a bivalent into univalents. All the bivalents at anaphase I separated synchronously to the poles and sometimes two separating elements, probably the homologues of a bivalent, continued to remain on the equatorial region when all others had nearly reached the poles. Metaphase II cells showed 29 univalents confirming the haploid number, n=29 (Figs. 8 to 10).

*Macroglossum bombylans**

2n=58. Metaphase I cells showed 29 bivalents. Though anaphase I was normal, in a good number of dividing cells, lagging behaviour of a bivalent was significant. Metaphase II cells showed 29 univalent chromosomes (Figs. 11 to 13).

*Macroglossum gyrans**

2n=58. Metaphase I cells showed 29 bivalents. In most cells one bivalent was deeply stained while occasionally an early separation of a bivalent to its components was seen. Anaphase I was normal. Metaphase II cells showed 29 univalents establishing the haploid number as n=29 (Figs. 14 to 16).

*Rhyncolaba acteus*

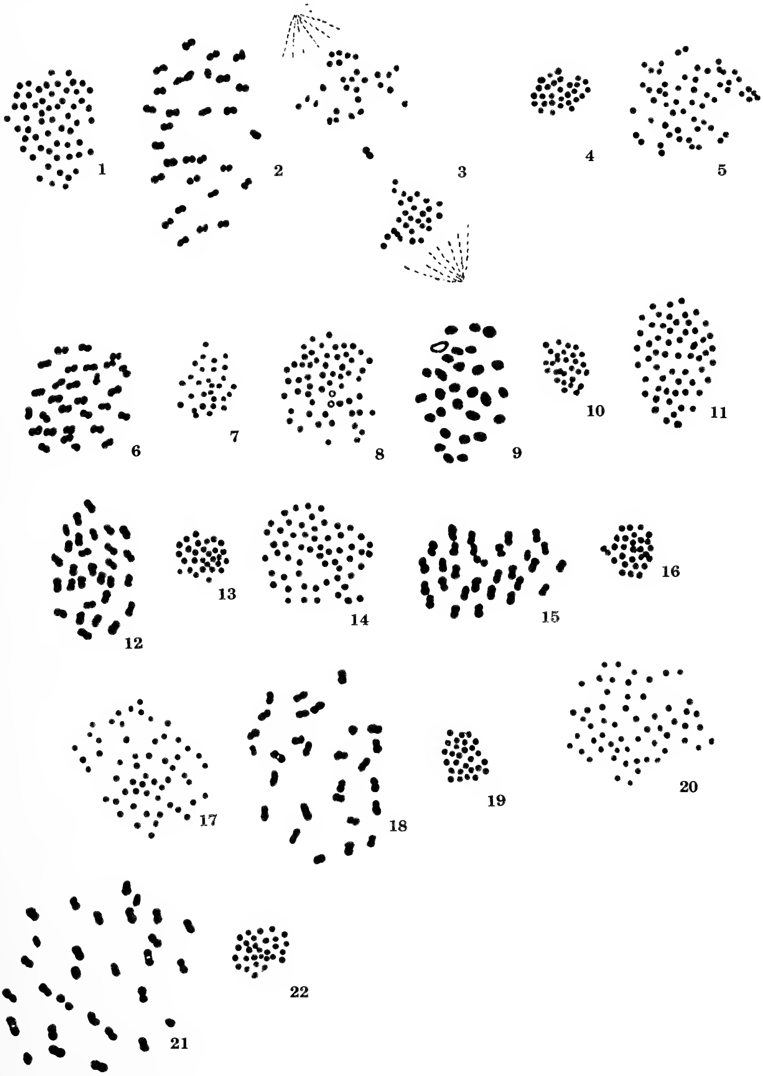
2n=56. Metaphase I cells showed 28 bivalents. Metaphase II showed 28 univalents. The present investigation, while recording a deviation in the chromosome number (n=28) of the species from the modal haploid number (n=29) for the family Sphingidae, also records a difference from the number (n=29) already recorded for this species by Rishi (1975) (Figs. 17 to 19).

*Theretra oldenlandiae*

2n=58. Metaphase I cells contained 29 bivalents. Precocious separation of a single bivalent into two univalents was apparent in many plates. Metaphase II showed 29 univalents. The haploid number n=29 determined for this species is at variance with n=31 reported by Gupta (1964) (Figs. 20 to 22).

## Discussion

The remarkable uniformity, except for minor details, in morphology and behaviour of lepidopteran chromosomes during the meiotic cycle have been well documented (Seiler, 1914; Beliajeff, 1930; Federley, 1928; Lorkovic, 1941; Gupta, 1964; Suomalainen, 1969b, 1971; Rishi, 1975;



Nayak, 1975). The present investigation agrees with the earlier published data. The chromosomes are minute, homomorphic and isodiametric, presenting a circular distribution in mitotic metaphase stages. In the family Sphingidae, 31 species have been cytologically investigated thus far and the modal haploid number for this family has been established as n=29 (Federley, 1928; Beliajeff, 1930; Saitoh, 1959, 1960; Robinson, 1971). The next most frequent numbers for this family are 28 and 27, while other numbers are 31, 33, 49, 52 and 59. The highest chromosome number in the family (n=59 in *Langia zenzeroides nawai*) has been reported by Saitoh and Kumagai (1973). It differed from all others in having the haploid number almost double that of the modal number (n=29)—a situation showing an indication of a phylogenetic peculiarity of this subspecies. In the present analysis, the haploid chromosome number ascertained in six out of seven Sphingid moths is uniformly 29, in accordance with the modal haploid number for the family. However, in one species, *Rhyncolaba acteus*, the base number has been determined to be less by one, i.e., n=28, although at variance with the observations made by Rishi (1973) who reported the chromosome number as n=29 for the same species. This deviation in chromosome number may be due to geographical variation. Similarly, a variation in the chromosome counts of *Theretra oldenlandae* has been recorded. While our observations establish the haploid number for this species as n=29, that of Gupta (1964) records it as n=31. This chromosome polymorphism as well may be due to geographical variation.

Analysis of sex chromosomes in Lepidoptera has been greatly impeded due to the homomorphic nature of the metaphase chromosomes which make the sex chromosomes and autosomes undifferentiable. In Lepidoptera, the female is the heterogametic sex with the XY (ZW) or XO (ZO) sex chromosome mechanism while the male is of the XX (ZZ) type. In other insect orders the males are usually the heterogamous sex. No definite information is available as to the manner in which the switchover from male to female heterogamety occurred in the Lepidoptera during evolution from their presumed mecopteroid ancestors.

A heteropycnotic pair of chromosomes associated with the nucleolus during the spermatogenesis of *Philosamia cynthia* was considered as the sex chromosome pair by Kawaguchi (1937) and earlier by Kurihara (1929). The large bivalent occurring in the chromosome garniture of some species of Lepidoptera has often been considered as the sex bivalent (Bauer, 1943; White, 1973; Suomalainen, 1969b, 1971; Ennis, 1976). Traut and Mosbacher (1968) distinguished the sex chromatin as a distinctly heteropycnotic body in the somatic interphase nuclei in the females of 70 out of 83 species they examined and took it as the Y-chromosome since the presence of such a body was not observed in the corresponding males. In our investigations, which have been confined to the males only, we could not observe any heteropycnotic element associated with the prophase nucleus during spermatogenesis, nor was there any large bivalent to be attributed a sex chromosome as upheld by Suomalainen (1969). However, during anaphase I in three out of the seven species of Sphingid moths investigated, a peculiar late separation of a pair of chromosomal elements was occasionally observed. The pair remained midway between the groups of separating chromosomes which had almost reached the poles. This pair may be suspected as the XX sex chromosome pair of the males in view of the occurrence of similar lagging behaviour shown by sex chromosomes in other groups of insects.

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# A New Species of *Mitoura* Scudder from Southern California (Lepidoptera: Lycaenidae)

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**Abstract.** A new species of *Mitoura* Scudder from southern California, *M. thornei*, is described and figured. The insect is isolated by geography and the use of a select hostplant. The larval host is the endemic Tecate cypress, *Cupressus forbesii* Jepson (Cupressaceae), with which the adults are intimately associated. Data regarding the insect's spatial and temporal distribution are presented, and the early stages are briefly discussed.

## Introduction

The use of Coniferae as a larval host is quite limited among the Nearctic Rhopalocera. Only *Neophasia* Behr (Pieridae), *Incisalia* Scudder (Lycaenidae), and *Mitoura* Scudder are known to utilize Pinaceae and Cupressaceae (Howe, 1975). Host specificity, as is commonly encountered in the genus *Mitoura (sensu stricto*, the Cupressaceae-feeders), has been shown to be a potentially useful tool in dealing with butterfly taxonomy (Downey, 1962). The discovery of the monophagous *Mitoura hesseli* Rawson and Ziegler (1950), as a sibling species of *M. gryneus* (Huebner), demonstrates this value (Johnson, 1978). For many species, host specialization has resulted in restriction of range to small areas of acceptable habitat. Subsequent isolation of these regions may in time be the basis of local population differentiation, and eventually even speciation.

A unique and highly localized population of *Mitoura* was discovered in the vicinity of Otay Mountain in southern San Diego County, California, several years ago. Its geographic isolation and close association with the endemic Tecate cypress (*Cupressus forbesii* Jepson) strongly suggested that the insect was distinct from its congeners. Not coincidentally, the Otay Mountain area has long been known for its high degree of floral endemicity. Subsequent to its discovery, the insect became the subject of investigation by Fred T. Thorne. The majority of the data herein presented represents his research efforts.

## Discovery

While working with Paul Ehrlich's *Euphydryas editha* (Bosiduval) population study group from Stanford University, Thorne collected a single male *Mitoura* near Lower Otay Lake, 26 February 1972. No *Mitoura* were previously known from cismontane southern California since hosts for neither *M. loki* (Skinner) nor *M. nelsoni* (Boisduval) occur here. The only possible cupressaceous host available was Tecate cypress.

Upon suggestion of Thorne, David Hawks, a local lepidopterist, kept a watchful eye and managed to collect several specimens of the *Mitoura* while on a San Diego Natural History Museum field trip to the northeast slope of Otay Mountain, 8 March 1974. The insect was indeed closely associated with the endemic cypress.

In the years that followed, several lepidopterists were able to sample the *Mitoura* population at Otay Mountain and the adjacent Little Cedar Canyon area near Lower Otay Lake. Fred Thorne was eventually successful in obtaining eggs from live females, and reared the insects through to maturity several times, carefully recording the life history and developmental periods required by the insect (Fig. 6).

As southern California represents one of the greatest concentrations of lepidopterists in the country, it is remarkable that this insect remained undiscovered until 1972. Inaccessibility to the Otay Mountain area was undoubtedly the major deterrent. Although much of the area is under the direct control of the Bureau of Land Management, rough dirt roads severely hinder travel; furthermore, private ownership of adjacent land and owner reluctance to allow access has inhibited collecting activities in the area.

Based on phenotypic characters, a highly selective host preference, and a unique ecological association, the Otay Mountain *Mitoura* appears to represent a distinct species and, accordingly, is herein described.

## Systematic Description

### **Mitoura thornei** J. W. Brown **new species**

Figure 1, Row b

**Male:** Forewing length $\bar{x} = 12.7$ mm (range 11.5-14.0 mm). Head, thorax, and abdomen dark brown. Thorax dorsally covered with fine, long, brown body scales, ventrally covered with light brown to whitish gray scales. Abdomen thickly clothed in short, lighter brown imbricate rows of hair. Antennae black with a thin white band at each segmental joint; club black with a white streak ventrally near the base. Palpi black with scattered white scales. Eyes dark brown encircled by a fine white line of scales. Dorsal surface of forewing rich reddish brown with dark brown shading on costal margin, basal and postbasal areas, apical and subapical areas, and along the outer margin. Major veins also indicated by dark brown scaling. Male scent pad well developed. Hindwings concolorous with forewings, with extensive basal and marginal darkening. A fine white submarginal line between $Cu_2$ and 2ndA. A very short, slender, black hair-like tail at the end of $Cu_1$, tipped with white; and a longer tail at the end of $Cu_2$. Ventral surface of forewing mahogany brown with faint traces of lavender overscaling, heavier near apical and basal areas. A well-defined white submarginal line composed of five dashes interrupted only by the major forewing

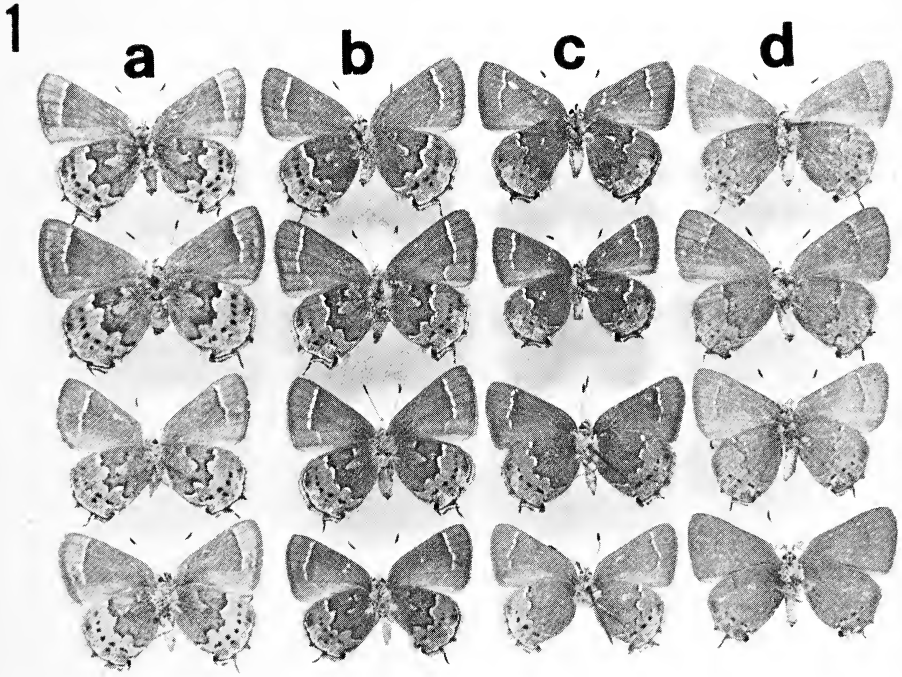

Fig. 1. Ventral aspect of four specimens of each of the related taxa: **a)** *Mitoura loki,* **b)** *M. thornei,* **c)** *M. nelsoni muiri,* **d)** *M. nelsoni nelsoni.*

veins. Offset basally is an additional longer, faint, white curved dash (present only in reared material) just below the well-defined line. Hindwings lustrous grayish lavender below, with a broad maroon-to-brown discal band. Rarely the entire surface is dusted with green overscaling. An irregular, though well-defined, white postmedian line at the outer edge of the discal band. A submarginal row of 6 (variable from 4 to 7) black terminal spots present in the light limbal zone. "*Thecla*" spot well defined. Terminal area between the row of black spots and the outer margin inconsistently marked with areas of heavy iridescent pale blue scaling.

**Female:** Forewing length $\bar{x}$ = 13.0 mm (range 11.5-14.0 mm). Similar in color and maculation to the male; without scent pad on upper surface of forewing.

**Genitalia:** Illustrated for both sexes of *M. thornei* and 3 related taxa, *M. loki, M. nelsoni,* and *M. nelsoni muiri* (Hy. Edwards) in Fig. 2. My analysis is based on two specimens of each sex of the four taxa. The drawings were made from the KOH macerated abdomens being placed in Hoyer's medium on temporary slides, and illustrated using a Wild 5A stereo microscope with drawing attachment. Thus artifacts of cover slips and positioning could be minimized.

The characters and their states were those employed by Johnson (1976b, 1978). On the basis of the limited samples, and the variation found, it would appear that

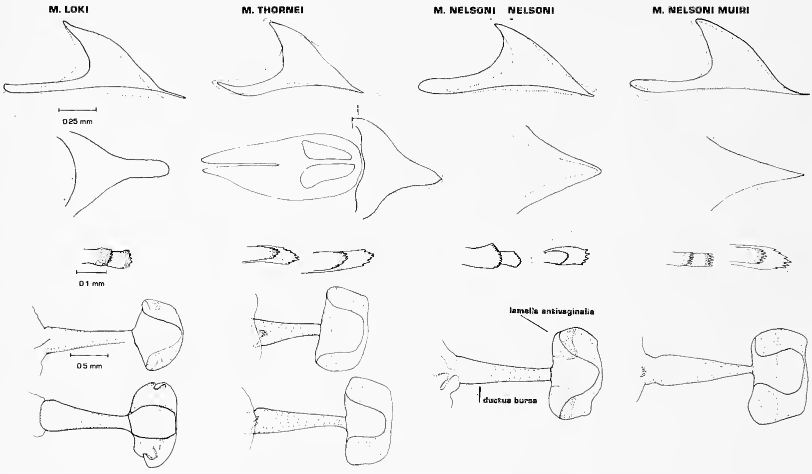

Fig. 2. Selected characters and variation in character states based on paired specimens of each of those related taxa: *M. loki, M. thornei, M. nelsoni nelsoni* and *M. nelsoni muiri.* **Top row**, valvae in lateral aspect. The first specimen drawn with solid line, the second with dotted line. **Second row**, saccus in ventral aspect (both *M. loki* identical, *M. thornei* showing valvae as well in ventral aspect). **Third row**, distal morphology of dorsal and ventral sets of cornuti (*M. loki* both identical). **Last rows,** with ductus bursa (sclerotized), and lamella antivaginalis in dorsal aspect. Portion of corpus bursae to left. *M. nelsoni* and *M. nelsoni muiri* specimens identical.

these characters do not provide reliable means to differentiate the entities. Preparation of longer series of material may well provide quantitative differences between populations, but these are in all probability meaningless as states upon which "species" or "subspecies" categories can be based. Refer particularly to the two ductus bursae samples of *M. thornei* and the dorsae and ventral sets of cornuti in *M. nelsoni*. Lateral shape of the valva are not of convincing value (e.g., *M. nelsoni*), although the construction in the caudal section of the corpus bursae of *M. nelsoni muiri*, consistent and unique in both specimens, is suggestive.

**Types:** Holotype, male, California, San Diego County, Little Cedar Canyon, north slope of San Ysidro Mountains (Otay Mountain), east end of Lower Otay Lake, 200 m, 32°37'N, 116°52'W, ex-female, ex-ovum, emerged 4 May 1980 (laboratory reared); allotype, female, same locality as holotype, ex-female, ex-ovum, emerged 28 October 1979 (laboratory reared). Described from 178 specimens collected and/or reared from 26 February 1972 to 6 March 1982.

**Disposition of types:** The holotype male and allotype are deposited in the collection of the San Diego Natural History Museum. Representative examples from the paratype series are deposited in the following institutions: California Academy of Sciences, San Francisco, California; Los Angeles County Museum of Natural History, Los Angeles, California; Allyn Museum of Entomology, Sarasota, Florida; American Musuem of Natural History, New York; United States National Museum, Washington, D.C.; and Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. Paratypes are also deposited in the following private collections: J. W. Tilden, San Jose, California; John Lane, Santa Cruz, California; and Fred Thorne, El Cajon, California. The remainder of the paratype series deposited in the collection of the San Diego Natural History Museum.

**Etymology:** The name *thornei* is derived from Fred T. Thorne. Mr. Thorne discovered and originally investigated this interesting insect. His work on the butterflies of San Diego County, California, and the Nearctic Theclinae is widely known and respected.

## Discussion

*Mitoura thornei* is isolated by geography and the use of a select hostplant. In southern California its closest relative appears to be *M. loki* (Fig. 1a) which it resembles in voltinism (multiple brooded), phenotype, and genitalic charcters. It is distinguishable from *M. loki* in host preference and in the color of the ventral hindwing surface. *M. thornei* is not similar in appearance to *M. nelsoni* (Fig. 1d); additionally, southern California populations of *M. nelsoni* are all univoltine. However, the use of a *Cupressus* species as the larval host suggests a close affinity with *M. nelsoni muiri* (Fig. 1c), an entity which some authors feel is worthy of specific consideration (Johnson, 1976b). The Otay Mountain *Mitoura* is phenotypically similar to *M. nelsoni muiri*; furthermore, these two insects occupy habitats that are quite similar although considerably disjunct (Fig. 3). *M. thornei* is easily distinguished from *M. nelsoni muiri* by the presence of markings in the basal area of the ventral hindwing; the basal area of *M. nelsoni muiri* is totally devoid of markings. Also, *M. nelsoni muiri* is univoltine (Opler and Langston, 1968). Although no sympatry occurs, *M. thornei* is separated from the nearest *M. loki* population by only about 60 km, and from the nearest *M. nelsoni* population by about 50 km.

The host for the Otay Mountain *Mitoura* is Tecate cypress, a closed-cone conifer which occurs on xeric slopes in the chaparral. Although possibly widespread in the Neocene (Axelrod, 1967), Tecate cypress is now restricted to a relatively few isolated stands extending from the Santa Ana Mountains of Orange County, California, south into northern Baja California, Mexico (Little, 1971) (Fig. 4). Where it occurs it is often the dominant plant, the trees generally surpassing most of their shrubby competitors in the chaparral community (Zedler, 1977). Fire plays an integral part in the natural history of these trees as it is the major factor that initiates cone opening and seed dispersal. Chaparral fires have undoubtedly caused great fluctuations in the population of both the cypress and the associated *Mitoura*. Although the insect is known only from the Otay Mountain area, it may possibly occur throughout the natural range of the host. A rather extensive stand of Tecate cypress occurring in the Sierra Peak-Coal Canyon area of northeastern Orange County appears

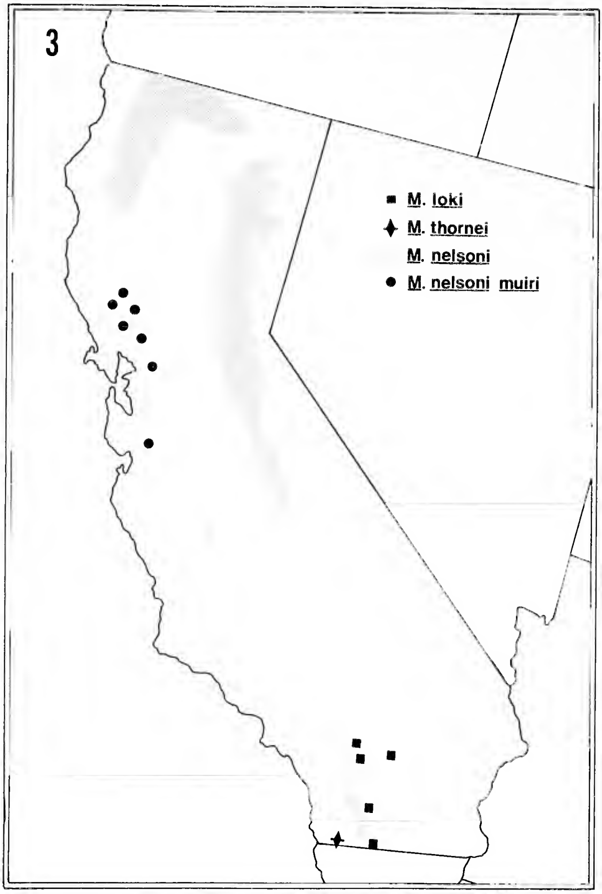

Fig. 3. General California distribution of the four related taxa discussed in the text. *M. loki* associated with *Juniperus californica* Carr.; *M. thornei* known only from Otay Mountain; *M. nelsoni* distributed throughout the range of *Calocedrus decurrens* (Torr.) Florin.; *M. nelsoni muiri* found only in association with *Cupressus sargentii* Jepson.

to provide an ideal habitat for the insect. However, limited sampling of the area (Orsak, 1977; Brown and Faulkner, personal observation) has failed to yield any *Mitoura*. It has been suggested that this stand of cypress represents an introduced population, but the available data indicates such is unlikely. The entire area was completely ravaged by chaparral fires in the recent past, which might possibly have eliminated any relict *Mitoura* population that formerly existed. Extraordinarily, a single specimen of *Mitoura* is known from Isla Guadalupe, over 230 km off the western coast of Baja California, Mexico (Powell, 1958). The insect has been determined

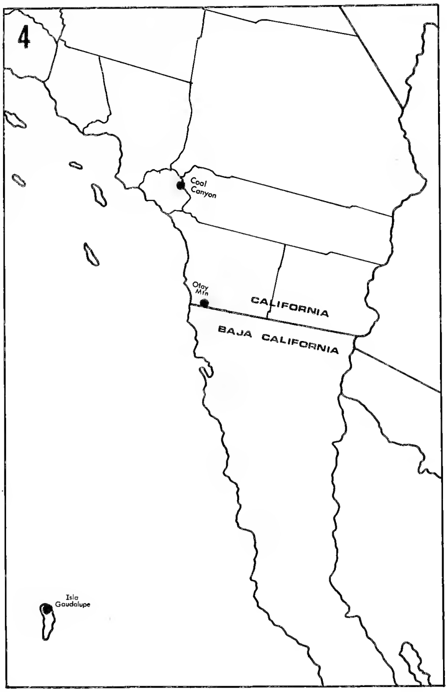

Fig. 4. Spatial distribution of *Cupressus forbesii.* Stippling represents stands of trees. Dots indicate localities mentioned in text.

by John Lane as *M. nelsoni muiri*, and the suspected larval host is the endemic, insular *Cupressus guadalupensis* S. Watson. However, many botanical taxonomists consider *C. guadalupensis* conspecific with *C. forbesii*; thus this Isla Guadalupe insect bears a biological affinity to *M. thornei*, at least in food plant usage.

*Mitoura thornei* appears to be at least double brooded; adults are on the wing in March and again in June (Fig. 5). Capture records indicate the second brood may only be a partial one, as is the case with *M. loki* and the eastern *M. gryneus* and *M. hesseli*. Phenotypically the two broods are similar, the summer brood being just slightly darker in color.

Although several nectar sources are utilized, adults are more commonly encountered by "tapping" the branches of the host tree. Males generally perch near the top branches and are quite easily disturbed. Their quick, erratic flight, however, makes them difficult to capture. Nectar sources include manzanita (*Arctostaphylos otayensis* Weis. and Schreib.), California or flat-top buckwheat (*Eriogonum fasciculatum* Bentham), and Yerba Santa (*Eriodictyon* sp.).

## Early Stages

The early stages of *M. thornei* closely resemble those described for *M. siva* (W. H. Edwards) (Coolidge, 1924), *M. loki* (Comstock and Dammers, 132a), and *M. nelsoni* (Comstock and Dammers, 1932b). Eggs, light green in color and echinoid in shape, are laid singly on the new growth of the host. The egg stage lasts 7 to 14 days (Fig. 6). The newly hatched larvae initially bore into the young stems of the host but become external feeders as they develop. Mature larvae closely resemble the terminal twigs on which they feed. Their color is vivid green with two irregular white crescents on each segment, one on either side of the middorsal crest; the markings together form a longitudinal stripe on each side of the body. Additionally, there is a thinner, more consistent longitudinal white stripe above the prolegs on each side of the larva. The entire body is covered with minute brown hairs. Complete larval development requires 26 to 35 days under laboratory conditions. Although females exhibit a distinct ovipositional preference for *Cupressus forbesii,* larvae will develop normally on California juniper (*Juniperus californica* Carr.) in the lab. The pupae are dark chestnut brown with fine mottling, and are covered with fine brown hairs; the wing cases are bare. Pupation generally occurs in the duff or debris at the base of the host trees (David Faulkner, personal communication).

## Conclusion

The genus *Mitoura* has been the subject of many taxonomic, biological, and regional studies, most recently by Clench (1981) and Johnson (1976a, 1976b, 1978). However, a number of unresolved problems still remain,

**5**

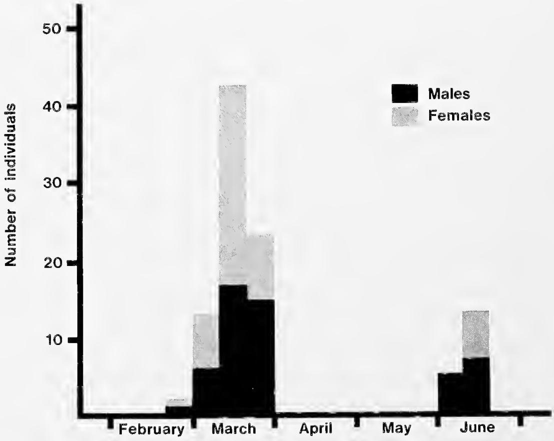

Fig. 5. Flight period graph of *Mitoura thornei* based on all wild caught adults examined.

particularly with the western populations of *M. siva* and *M. nelsoni*, and no taxonomic diagnosis of the species complex is widely accepted. Johnson (1976b) suggests a standard method for species assessment using characters of wing color and maculation, genitalia, and food plant usage. Unfortunately, recent workers, including Johnson, have relied almost exclusively on genitalic characters and, in general, have included other information only in support of their genitalic diagnosis. The limited data presented above (Genitalia) indicates that the genitalia of *Mitoura* are of very limited taxonomic significance, certainly in a practical sense, and other criteria must be used in attempting to understand relationships and phylogeny. Furthermore, conclusions concerning "isolating mechanisms" based on these cryptic differences are certainly meaningless (Shapiro, 1978). Lafontaine (1981), in classifying a group of *Euxoa* Huebner (Noctuidae), which as *Mitoura* showed substantial patterns of variation with minor differentiation of genitalia, was able to construct a convincing phylogeny by careful methodology. Our understanding of *Mitoura* has not yet progressed as far. In the closely related genus *Callophrys* Billberg, often considered congeneric with *Mitoura*, the genitalia are also of little or no value in distinguishing the species (Dornfeld, 1980). Although genitalic characters of *M. thornei* do not convincingly separate it from either *M. loki* or *M. nelsoni*, wing color and maculation, host specificity, and asynchronous peak flight periods do clearly distinguish these closely related entities.

**6**

| BROOD YEAR | FIRST OVA LAID | FIRST EGG HATCH | DAYS IN OVUM | FIRST PUPAE | LARVAL DAYS | FIRST IMAGO | PUPAL DAYS | TOTAL DAYS IN CYCLE |
|---|---|---|---|---|---|---|---|---|
| 1976 | 20.III.76 | 1.IV.76 | 11 | 3.V.76 | 33 | 15.V.76 | 12 | 56 |
| 1977 | 18.VI.77 | 25.VI.77 | 7 | 23.VII.77 | 28 | 3.VIII.77 | 11 | 46 |
| 1978 | 11.VI.78 | 18.VI.78 | 7 | 22.VII.78 | 34 | 15.II.79 | 208 | 249 |
| 1979 | 9.III.79 | 21.III.79 | 12 | 16.IV.79 | 26 | 2.V.79 | 16 | 54 |
| 1980 | 5.III.80 | 19.III.80 | 14 | 23.IV.80 | 35 | 6.VII.80 | 42 | 92 |

Fig. 6. Developmental periods required by *M. thornei*. Data from broods reared by Fred Thorne.

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# Commentary on Miller and Brown vs. Ehrlich and Murphy *et al.*: Pluralism in Systematics and the World-wide Nature of Kinship Groups

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## Introduction

*The Journal of Research on the Lepidoptera* has invited comment on Ehrlich and Murphy's (1982) critique of and counterproposal to the nomenclature proposed by Miller and Brown (1981) for the butterflies of North America north of Mexico. Ehrlich has published significantly on taxonomic characters and the higher classification of butterflies (Ehrlich, 1958) and has also co-edited a popular guide to North American butterflies utilizing a nomenclature different from that proposed by Miller and Brown (Ehrlich and Ehrlich, 1961). Ehrlich and Murphy, citing in their acknowledgments the support of some fifty professional and amateur lepidopterists, take particular exception to the number of new generic names introduced in binomial combinations by Miller and Brown. They go beyond suggesting these new combinations be ignored, and propose a standardization of common usage for binomials based on another work, that of Howe (1975).

Ehrlich and Murphy's critique is derived from and characterized by certain concepts and methodological viewpoints. Therefore, it is important that lepidopterists (especially systematists and biogeographers) scrutinize the validity and comprehensiveness of their arguments to determine whether their proposals are appropriate and acceptable. Without scrutiny from diverse points of view, particular arguments may seem persuasive, but actually lack the comprehensiveness needed to arbitrate the kind of controversy that has occurred since the publication of Miller and Brown.

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[1] Both authors do research supported by grants affiliated with the American Museum of Natural History. Johnson is a Research Associate of the American Museum of Natural History and the University of Wisconsin Museum of Natural History. The opinions given are solely those of the authors.

Underlying our particular response are two points of reference quite different from those of Ehrlich and Murphy. Their primary concern is the stability of nomenclature in one group of insects (butterflies) on part of one continent (North America north of Mexico). As persons with professional training specialized in systematics and with study groups characterized by worldwide distributions, our inclination is toward studying Lepidoptera taxonomy within the context of systematics as a whole, and with a view of North American Lepidoptera as one component of worldwide patterns of distribution and kinship.

## Areas for Discussion

We suggest four areas of discussion, each of which will be examined in separate sections under the following headings with illustrations and examples provided:

(1). "Appropriate Arbitration"—Can the controversy concerning a preferred nomenclature for North American butterflies be arbitrated and, if so, are Ehrlich and Murphy appropriate arbiters?

(2). "Pluralism in Systematics"—Are the arguments and proposals of Ehrlich and Murphy congruent with contemporaneous systematic theories?

(3). "The Worldwide Nature of Kinship Groups"—If continents are single components of worldwide patterns of distribution and kinship, must nomenclature include recognition of those patterns?

(4). "Practical Problems"—Do the proposals of Ehrlich and Murphy have practical problems, especially the possibility of inadvertant suppression of alternative points of view?

The above-mentioned areas of discussion are suggested because of an overall problem we perceive in the presentation by Ehrlich and Murphy: that areas of probable general agreement also inherently contain severe problems of specific interpretation. Ehrlich and Murphy make several major points with which we think most systematists would agree and which have probably attracted broadest support. It may be less apparent, however, that matters of language and interpretation in these views lead almost inevitably to serious divergences of opinion depending on the particular theoretical preferences of researchers.

For example, significant points are strongly voiced by Ehrlich and Murphy (pp. 4-7), particularly their observation that problems could ensue if part of the professional and amateur community adopt Miller and Brown's nomenclature while others retain that of Howe or some other author. Nearly all systematists would agree that new combinations or changes of status introduced in checklists or popular works should be based upon properly documented revisionary works. Changes of status or combinations without proper data and arguments, or even including the latter but encompassing only one or a few taxa of a group, introduce potentially serious synonymic problems into the scientific literature. Most specialists would also agree with Ehrlich and Murphy that proliferation of new generic names in binomial combinations is probably less preferable than possible alternatives. However, there exists a diversity of opinion concerning what constitutes competence in taxonomic works and the various methodologies for producing them. Similarly, when Ehrlich and Murphy cite particular examples of combinations and groupings of taxa in North America in relation to their own theoretical preferences concerning taxonomic and geographic convenience (pp. 2-4), they also elicit potential controversy in methodological interpretation. Since the problem of generic group names is the crux of the issue addressed by Ehrlich and Murphy, we have arranged our entries in a format which addresses this problem.

### *Appropriate Arbitration.*

After establishing that a controversy exists concerning North American butterfly nomenclature, Ehrlich and Murphy take two actions which, in effect, propose that they be potential arbiters. Firstly, they suggest that a preferred nomenclature (Howe, *loc. cit.*) might be chosen [through the Lepidopterists Society], explain how this standardization would be enforced, and provide details concerning criteria and exceptions that could be allowed. Secondly, they offer scientific arguments drawn from their particular theoretical preferences in systematics and biogeography, support adoption of a nomenclature similar to that authored in Ehrlich and Ehrlich (*loc. cit.*) and cite other work of Ehrlich (*loc. cit.*) as corroboration for the appropriateness of their view.

Inquiry concerning whether other considerations, implications, or possible consequences may render a standardized nomenclature undesirable, or whether the surrounding controversy can be appropriately arbitrated, are not the primary concern of their paper. Such consideration has been aided by the actions of editors of *The Journal of Research on the Lepidoptera* in inviting comment. In our view, the most important problem concerning possible arbitration of the controversy is whether any point of reference among possible opinions is sufficiently broad to be considered appropriate. Within this context, the worthiness of Ehrlich and Murphy's arguments should be considered.

### *Pluralism in Systematics.*

Pluralism refers to the existence of many and diverse points of view and allows for the possibility that each might be valid. We believe it is inevitable that there will be strong differences of opinion in systematic theory and that many points of view will be argued as "scientifically" the "best" or most preferable. The case arises because systematic theories and methodologies begin with certain assumptions and develop the logic of technique, argument, and inference from them. Table 1 reviews some of the basic, but very different, kinds of assumptions and generalizations preferred by the three most widely pursued schools of systematic theory. It seems not only inevitable that these differences will remain, but that the taxonomic results of each of these methodologies will contribute different groupings of taxa that will be incorporated into checklists and popular works.

Though the topic of systematic theory and methodology is vast, three particular areas deserve mention in relation to the issues addressed by Ehrlich and Murphy.

(a). *Divergent Theories and Methods in Systematics*—Relevant to the discussion of Ehrlich and Murphy is that among the three schools listed in Table 1 there is little agreement concerning basics—criteria for species and genera, validity of biologically defined or investigated taxa, criteria for placing taxa into groups, the nature of relatedness (kinship or similarity) [see below], the relation of kinship to a classification, the relation of nomenclature to a classification, the relation of systematics to spatial (biogeographic) considerations, and stability.

(b). *Different Concepts of Relatedness*—The function of each of the methodologies listed in Table 1 is to group organisms in appropriate ways, a concern also voiced by Ehrlich and Murphy. The argument between the schools, like the argument between Ehrlich and Murphy vs. Miller and Brown, concerns which way of grouping is "better". One standard of "better", that of "relative monophyly", is examined to a limited degree in Table 2 (see Schuh and Polhemus, 1980 and Sneath and Sokal, 1973, for different technical opinions on systematic methods and evaluations of the importance of monophyly). Both Miller and Brown, in the introduction to their checklist, and Ehrlich and Murphy, in their arguments, cite the importance of monophyly and their emphasis on this criterion in preparing their works. Monophyly concerns which grouping of taxa actually contains the most related of organisms.[2] However, "relatedness" is not defined identically by the various schools of systematics. It is a matter of opinion whether "relatedness" implies a relationship of "similarity" (most alike in taxonomic characters) or a phylogenetic relationship (a relationship of kinship, that is, descendants of an immediate common ancestor). Regardless of this problem, the grouping of kinds of organisms from one continent alone will inevitably lead to unrelatedness in the grouping if more immediately related groups occur on other continents.

Table 2 shows that, when one of the groups cited by Ehrlich and Murphy as an example of the problem of taxonomic convenience (*Callophrys sens. lat.*, p. 3), is analyzed by different systematic methods, and includes patterns of most immediate kin on continents other than North America,

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[2] Because of differences in the concept of "relatedness" we have not chosen to quote any particular rigorous definition of monophyly. Such could be located in the methodological papers cited in this paper or in the standard texts of the schools of systematic theory.

## TABLE 1. SCHOOLS OF SYSTEMATIC THEORY

| Features | Evolutionary | Phenetic | Phylogenetic |
|---|---|---|---|
| Well known founders/proponents | Simpson, Mayr *et al.* | Sokal, Sneath *et al.* | Hennig *et al.* |
| Commonly known as— | "traditional taxonomy" | "numerical taxonomy" | "cladistics" |
| View of ancestors | can be recognized, only sometimes hypothetical | can be recognized | cannot be recognized, hypothetical only |
| View of speciation | allopatric speciation and phyletic gradualism | phylogeny viewed as unrecoverable | allopatric speciation not phyletic gradualism |
| General method of grouping taxa | weighted similarity | equally weighted similarity | shared unique characters (derived characters) |
| View of monophyly | taxa need not be precisely monophyletic | phylogeny irrelevant as criterion for grouping | must be precisely monophyletic |
| Relation of phylogeny to classification | phylogeny not necessarily to be retrievable from classification | phylogeny irrelevant | phylogeny must be retrievable from classification |
| View of utility of classification | to express divergence or phylogeny | usefulness and convenience | to express hypothetical phylogeny |
| Name of branching diagram | evolutionary tree | phenogram | cladogram |
| View of relation of classification to distribution (geographic) | none necessarily | none | expected to correlate with allopatry |
| Preferred biogeographical school of theory | dispersal biogeography | dispersal biogeography | vicariance biogeography |
| View of subspecies | relevant | relevant | irrelevant |
| View of biological species definition | conceptual and methodological tool | conceptual and methodological tool | conceptual tool only |
| View of tests of reproductive compatibility (see above) | relevant | relevant | irrelevant |
| Common catch words | divergence, distance, adaptive zones, weight, gradualism, gradism, tree, biological species, etc. | OTU, similarity, convenience, distance, biological species, biological investigations, etc. | apomorphy, plesiomorphy, clade, splitting events, polarity, monophyly, rank, etc. |
| General time period | 1940- | 1960- | 1970- |
| Contribution of groupings to current checklists (butterflies) | circa 90% | circa 10% | circa 2% |

monophyly is difficult to assess equitably. According to the assessment of the cladistic methodology, in the case of Callophryina[3], Miller and Brown's classification appears superior, containing nine monophyletic groups and three "paraphyletic" groups (groups in which only one unrelated taxon has been included by mistake[4]). Howe's classification for the same group, preferred by Ehrlich and Murphy, is (except for genera containing only one species) entirely "polyphyletic" (made of groups all having more than one

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[3] Genera listed in Table 2 comprise one monophyletic assemblage defined as an infratribe "Callophyrina" within the Tribe Eumaeini (sensu Eliot, 1975) according to Johnson, 1981. See footnotes and explanation of Table 2 for comments on the limitations of these data.

[4] For particular rigorous definitions and discussion of monophyly, paraphyly, and polyphyly see Nelson, 1971; Ashlock, 1971.

## Table 2. NOMENCLATURE AND MONOPHYLY

North American vs. Worldwide

### Taxonomic Rudiments of an Intercontinental Kinship Group

**Components:**

| **Taxon** | **Assessment of Relative Monophyly by Cladistic Analysis** | | | **Name and Location of Most Immediate Kinship Group** |
|---|---|---|---|---|
| | **Howe** | **Miller/Brown** | **Cladistic** | |
| *Incisalia* sens. strict. | polyphyletic | monophyletic | monophyletic | new genus, China |
| *Incisalia* sens. lat. | polyphyletic | paraphyletic | monophyletic | new genus, South America (A)<br>*Satsuma***, China (P) |
| *Mitoura* sens. strict. | polyphyletic | monophyletic | monophyletic | *Callophrys*, North America-Eurasia |
| *Mitoura* sens. lat. | polyphyletic | monophyletic | monophyletic | *Callophyrs*, North America-Eurasia |
| *Callophrys* sens. strict. | polyphyletic | monophyletic* | monophyletic | *Mitoura*, North America |
| *Callophrys* sens. lat. | polyphyletic | monophyletic* | monophyletic | *Mitoura*, North America |
| *Satsuma*** sens. strict. | left out arbitrarily | left out arbitrarily | monophyletic | *Sandia*, North America |
| *Satsuma*** sens. lat. | left out arbitrarily | left out arbitrarily | monophyletic | *Sandia*, North America; newgenus, Andes, South America |
| *Cyanophrys* sens. strict. | polyphyletic | paraphyletic | monophyletic | new genus, South America |
| *Cyanophrys* sens. lat. | polyphyletic | paraphyletic | monophyletic | *Sandia*, Central & South America; new genus, South America |
| *Sandia* sens. strict. | monotypic in polyphyletic assemblage | monotypic monophyletic | monophyletic | new genus, South America |
| *Sandia* sens. lat. | monotypic in polyphyletic assemblage | monotypic monophyletic | monophyletic | new genus, South America |
| *Xamia* sens. strict. | monotypic in polyphyletic assemblage | monotypic monophyletic | synonymized with *Sandia* | new genus, South America |
| *Xamia* sens. lat. | monotypic in polyphyletic assemblage | monotypic monophyletic | synonymized with *Sandia* | new genus, South America |
| *culminicola* Group, of *Thecla**** sens. strict. | left out arbitrarily | left out arbitrarily**** | monophyletic | *Satsuma***, China |
| *culminicola* Group, of *Thecla**** sens. lat. | left out arbitrarily | left out aritrarily**** | monophyletic | *Satsuma***, China |
| new North American genera | 0 | 0 | 0 | |
| new Eurasian genera | —— | —— | 3 | new genus, Central America; *Incisalia* sens. strict., North America |
| new Central & South American genera | —— | —— | 4 | new genus, South America; *Cyanophrys* sens. strict. and sens. lat., Central & South America; *Satsuma***, China |

We use sens. strict. to refer to the immediate kinship group (clade) of the type species; we use sens. lat. to refer to the remaining assemblages within the genus which may be one (part of a paraphyletic assemblage) or more than one (part of a polyphyletic assemblage).

*We allow that the well known Eurasian taxa are left out by the arbitrary nature of the checklist.

***Satsuma* = *Ginzia*

***Draudt, in Seitz (1919)

****Brown (1942) noted that this group was probably in the same overall monophyletic assemblage as North American *Incisalia* sens. lat.

In assemblages made up of three groups it is of interest to note which relation is apotypic (A)—most immediate kinship group with relatively more-derived characters—and which is plesiotypic (P)—most immediate kinship group with relatively more-primitive characters.

Table 2. Summarizes monophyly as assessed by one particular cladistic analysis (Johnson, 1981) compared to classifications in Howe (1975) and Miller and Brown (1981) for taxonomic components of the "*Callophrys*" *sens. lat.* as described in the text. The following qualifications are important to understanding the nature and limitations of the comparison. If the intercontinental kinship relations of this particular study group show either Miller and Brown's or Howe's classification to be more or less monophyletic in comparison, it may result A) simply from chance alone since both continentally restricted classifications are arbitrary to that extent or B) because arbitrarily using separate genera (but not monotypic ones) instead of clusters of subgenera within one genus is less prone to para- or polyphyly, since if some groups are actually more immediately related to components on another continent, they are free to be associated without contradicting a pre-existing arbitrary subgrouping. As a cladistic study the relationships posited represent a hypothesis of kinship relations and are open to claims of counter-evidence or refutation by other alternative cladistic interpretations, use of another method, refutation of the interpretation of characters or character states, implications of additional characters, implications of additional taxa, and/or implications of additional distributional data. The hypothesis indicated by our interpretation (our cladogram) is supported by the least contradictory interpretation of several hundred characters and character states in just over two hundred taxa distributed on five continents and two additional subregions. It does not, therefore, claim to be "right", but simply one hypothesis of relationships derived from the data.

unrelated group mistakenly included and of which none are most directly related to each other[4]).

Another researcher (James Miller, pers. comm.), also using the cladistic methodology as a point of reference regarding the genus *Papilio* on a worldwide basis (Ehrlich and Murphy, pp. 6-7), offers a different point of view. Although he does not think Howe cites characters appropriate to erecting genera or monophyletic groups, at face value the Howe classification contains more monophyletic unity than that of Miller and Brown. The point demonstrated by these two examples is that not only is the criterion "better" difficult to equitably assess among lists of purportedly related species, its assessment depends on rather arbitrary points of view. The footnotes and explanation of Table 2 explain to some degree the particular arbitrary assumptions and definitions used by us to cladistically evaluate the groupings preferred by the other authors. To the extent that a preferred nomenclature for one continent would tend to favor one such arbitrary concept of relatedness, we pursue a discussion of the frequency of intercontinental relations of North American butterflies in the next entry.

Another comment is relevant to the question of defining relatedness. It regards the extent to which lepidopterists infer actual phylogenetic (kinship) relationships between taxa based on their order in checklists. If lepidopterists view these groupings, or their linear order, as implying estimations of kinship relations, creation of a preferred nomenclature for one continent will create some indeterminate number of spurious groupings. On the other hand, if lepidopterists do not imply any kind of relatedness to such groupings one has to question why a controversy exists over groupings at all. Regarding the above observation it might be best if such listings were alphabetical or chronological according to dates of description. The phenetic school of systematic methodology prefers that no claim of phylogenetic relationship be a requirement for grouping itself (see Cracraft, 1974). The interest of Ehrlich and Murphy in convenience is probably based on this view, as opposed to other systematic positions which view convenience as secondary in importance to attempts to define natural (e.g. kinship related) groups (see Nelson, 1970, and Colless, 1967, 1969).

(c). *Different Views on Generic Splitting*—Unfortunately, the views concerning formation of generic level taxa differ. Figure 1 illustrates this point relative to a paper by Clench (1978) and another opinion formulated by us for the sake of example. Clench, using a concept of relatedness based on simlarity, concluded that the taxa listed in Figure 1 are so similar that they can best be represented as belonging to one named group. This concept of similarity as a criterion for grouping is called a "grade". Clench concluded that the relations of these taxa are best expressed as one grade. If, however, hypotheses of kinship ("clades") are preferred over grades as a measure of relatedness, another worker would prefer that all the names be available so that the most informative branching diagram can be constructed for kinship relations within the group. The point demonstrated is that any decisions concerning lumping or splitting genera are purely arbitrary, depending on theoretical preference.

### *The Worldwide Nature of Kinship Groups.*

Table 2 summarizes the genera recognized by various authors in regard to the "*Incisalia-Callophrys*" "disagreement" cited by Ehrlich and Murphy (p. 3). The worldwide components of the group belong to one infratribe (Callophryina, *sensu* Johnson, *loc. cit.*) within the lycaenid tribe Eumaeini. Since we can only use published names for the groups we have

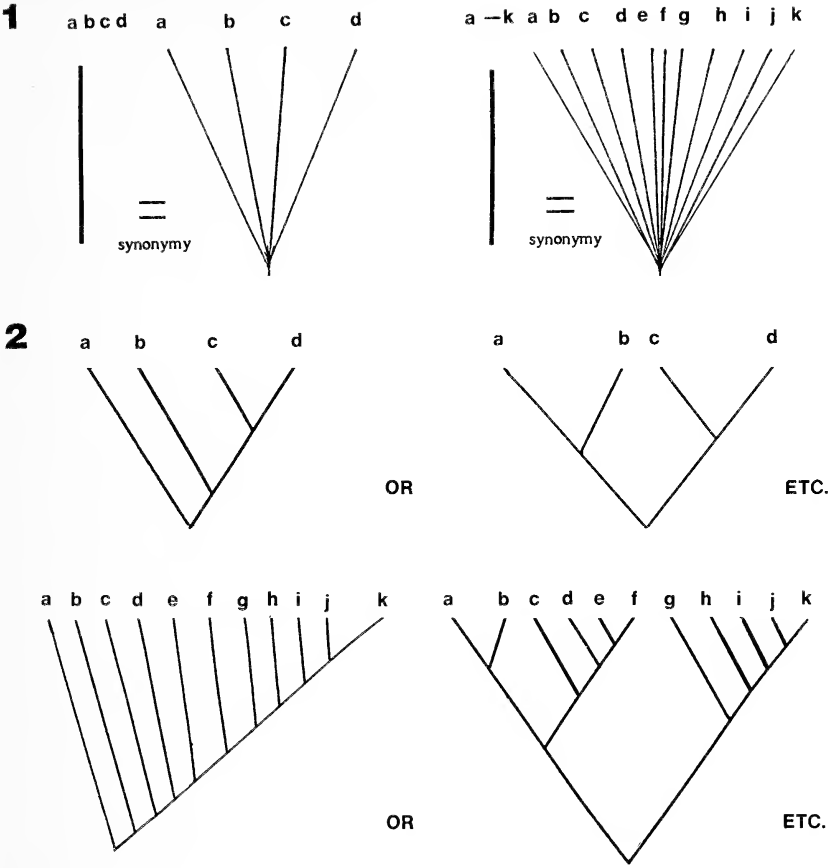


Fig. 1. Holarctic hairstreak genera viewed as a grade (1) and as clades (2). Though genera synonymized by Clench (1978) are acknowledgably similar, phylogenetic inference and retrievability are influenced by the lumping (1) or splitting (2) according to theoretical preference. In (1) lumping to one grade implies the components are retrievable as only one lineage. Maintenance of all the names (2) allows multiple expressions of phylogenetic components upon further analysis. (1) According to Clench *Fixsenia* (a) = *Strymonidia* (b) = *Euristrymon* (c) = *Thecla, Nordmannia,* etc. of authors, in part (d) (left) and *Satyrium* (a) = *Callipsyche* (b) = *Neolycaena* (c) = *Nordmannia* (d) = *Chattendenia* (e) = *Tuttiola* (f) = *Superflua* (g) = *Pseudothecla* (h) = *Bakeria* (i) = *Necovatia* (j) = *Thecla, Strymon, Strymonidia* etc. of authors, in part (k) (right). (2) If the above names are not synonymized but left to be used as subgroupings of the oldest names available (*Fixsenia/Satyrium*) phylogenetic retrieval of the subgroupings is facilitated (above and below, respectively, as two of many possibilities).

chosen the terms *sensu stricto* and *sensu lato* (as defined at the base of Table 2) to acknowledge additional components within each of the taxa listed in the left hand column of the Table. If certain taxa defined by exclusive North American criteria are either para- or polyphyletic[4] in an intercontinental context, it will be of interest to show to what non-North American components these groups are most closely related (right hand column in the Table).

An examination of Table 2 shows that within the intercontinental group studied, numerous groups actually have closer relatives on another continent. Whereas most lepidopterists are aware of European-North American relations (e.g. North American *Callophrys* always has been known to have related species in Europe), western North American-Asian relations are less well known. In the case of several groups in Table 2, western North American-Chinese relations are evident and have further components in western Central America and western South America.

When North America is considered alone, *Incisalia* seems like a homogeneous group of "brown elfins with mottled brown undersides". Actually the kinship components (here called *Incisalia sensu stricto* for the gymnosperm-feeders related to the type species, and *Incisalia sensu lato* for the angiosperm-feeders) each have their closest relative in China. The "genus" *Cyanophrys*, including the species *goodsoni* and *miserabilis*, happens (like Ehrlich and Murphy's example of *Pieris brassicae*) to have a type species that is the most morphologically specialized within its group. This inevitably restricts the use of *Cyanophrys* as a category. An additional problem arises because the genus was created by Clench for the sake of its North American novelties. Clench never listed what was to be included in *Cyanophrys*. We mention this not to fault Clench, but to illustrate that the creation of a new genus, *Cyanophrys*, for the sake of a few apparently unique North American butterflies, could not by nature anticipate that upon further analysis it would prove to be a polyphyletic assemblage. Study of morphology beyond that of wing characters, summarized in Table 2, indicates that taxa often placed with *Cyanophrys*, through association with its type species and North American representatives, actually include one group akin to *Sandia*, another very primitive group (including *goodsoni*) with kin in China, some kin in South America, and the more familiar "blue above and green beneath" hairstreaks of South and Central America which indeed can be grouped with *Cyanophrys sensu stricto*.

Table 2 also contains examples of genera described to include single North American species (*Xamia* and *Sandia*), disregarding the place of occurrence of their nearest relative, namely *Xamia* in Guatemala and *Sandia* in numerous parts of Central and South America. As long as North America is considered in isolation, both *Xamia* and *Sandia* are obvious "uniques" and considered worthy of subgeneric (Howe) or generic rank (Miller and Brown). Within their intercontinental kinship group, however, they belong to a broader generic level assemblage which is recognized only by considerable fragmentation of presently accepted classifications.

The data set examined in Table 2 suggests rudiments of what may be general patterns once additional worldwide groups are studied. It would be unfortunate if progress toward finding general patterns in worldwide phylogenetic and distributional relations, certainly the cornerstone of modern systematics and biogeography, was inadvertantly hampered by certain presuppositions about generic concepts derived from the study of only one region.

### *Practical Problems.*

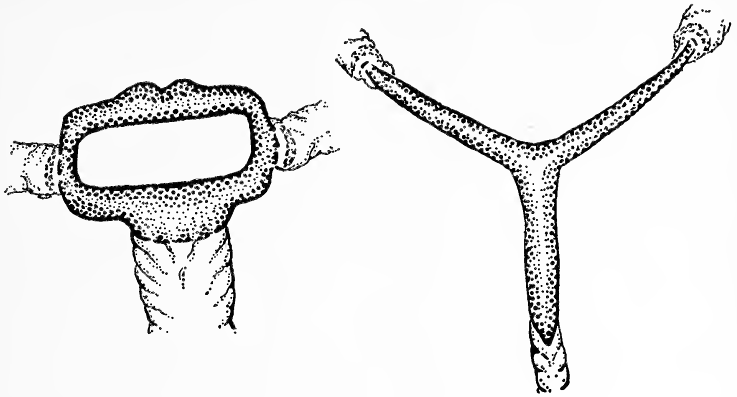
Several aspects in the proposals of Ehrlich and Murphy suggest practical problems of potentially serious consequence. Their presentation includes specific proposals for establishing a preferred nomenclature for North American butterflies and also commentary on their particular personal preferences in technique and methodology. Both suggestions have practical problems.

Perusal of Table 1 indicates other causes for concern, among them the problem of evaluating biological species and the differences of opinion concerning the kinds of testing for these. Two schools (phenetic and evolutionary) accept tests of reproductive compatibility as relevant to their methods; another (cladistics) rejects them *not* as irrelevant to biology, but inconsistent with the kinds of information usable in the method (Rosen, 1979). The frequency of such tests as criteria of specificity in Howe (*loc. cit.*) suggests this is a potential problem. Subspecies represent another problem. Two schools (phenetic and evolutionary) accept them as potentially useful, while the other (cladistic) cannot allow them on methodological grounds alone (Rosen, *loc. cit.*). The critical issue of monophyly is yet another problem. Evolutionary systematics allows paraphyletic groups while cladistics does not, and phylogeny is irrelevant to the main reason for grouping in phenetics.

The most important consideration concerning the above-mentioned problems is determining when exceptions to a preferred nomenclature would be allowed. Ehrlich and Murphy comment briefly that clear demonstrations of polyphyly will be an exception to their rules for encouraging editors and reviewers to "routinely reject any work that suggests generic name changes from those in Howe" (p. 8). Detailed demonstrations of polyphyly, aside from theoretical differences concerning their definition, usually are presented in lengthy revisionary works published by monograph series and research institutions. Such demonstrations are less apt to appear in the shorter studies usually published by society supported journals. Since Ehrlich and Murphy suggest that their rule would be instituted by legislation through the Lepidopterists Society a predicament is created for busy editors and reviewers. They would be required to consult source material for nomenclatures used or cited which are at variance with the standardized classification. This kind of discretion would require not only ready access to recent sources (not always possible), but training contemporary enough to allow fair assessment of the theories and methodologies from which the proposed nomenclature was derived. The latter may be circumstantially impossible for a researcher whose training is not in systematics, but in some related field of biology. In such cases "routine rejection" may overcome fairness since ignoring the new nomenclature causes neither controversy nor introduces into that society's journal an unfamiliar classification. An extreme result of such practices could be the development of two nomenclatures for North American butterflies—one preferred as convenient by the lepidopterists and another (open to change) of interest to systematists and biogeographers whose main concerns are systematic theory and spatial patterns transcending single continents. The latter situation has the same unfortunate consequence Ehrlich and Murpy seek to avoid by establishing Howe as a preferred nomenclature to Miller and Brown.

There are examples of how "accepted" classifications have led to repression of another author's work. The particular example we cite also addresses Ehrlich and Murphy's comments on the value of various characters. Our example concerns the very familiar Neotropical genera *Agrias, Prepona,* and *Anaea* (Nymphalidae) and the work of A. H. B. Rydon. These three genera are examples of "sacro-sanct" taxa which are generally assumed by lepidopterists to be monophyletic. They are also groups in which the female genitalia have only recently been studied (Johnson and Descimon, in prep.). It is important to note that very few studies of female genitalia (and many other important morphological characters, e.g. palpi, antennae, facial features, integumental androconia, etc.) have been made for North American butterflies. It is obvious that in the intercontinental study of Lepidoptera, components in less studied geographic regions will initially require the most fundamental taxonomic techniques ("alpha taxonomy" *sensu* Mayr, Linsley, and Usinger, 1953). It is unreasonable, therefore, that workers on one continent suggest limiting the use of certain fundamental morphological structures in regard to new groupings of taxa.

Figure 2 illustrates the occurrence of two very different configurations of the female genital plate in *Agrias, Prepona* and *Anaea*. These structures would lead almost any systematist to question whether these genera as presently defined could be monophyletic. A cladist would expect that one branching diagram be able to contain a hierarchy of these variants (along with those of other characters) with minimum contradiction. Such a branching diagram of monophyletic groups in this assemblage would require the erection of more genera if any of the groups are polyphyletic (which at least two seem to be, the other being paraphyletic). In 1961, A.



| | 1 | 2 |
|---|---|---|
| AGRIAS | X | X |
| ANAEA | X | X |
| PREPONA | X | X |

Fig. 2. Basic configurations of the female genital plate and their occurrence in *Agrias, Prepona,* and *Anaea* as defined by Comstock, 1961, and Seitz, 1919. Distribution of two very different configurations in the three "genera" indicates none are monophyletic, an observation corroborated by characters of the larvae (Rydon, 1971).

H. B. Rydon noticed the problem in these genera from characters in the larvae. He noted that drawings of Neotropical larvae by Ms. Margaret Fountaine and the Rev. Miles Moss in the library of the British Museum (Natural History) showed very obvious differences seeming to occur at random within Comstock's (1961) definitions of *Anaea* and its "subgenera." Rydon's conclusion was that *Anaea* could not be one group, since not only did the two very different character types occur within it, they occurred also in some *Agrias* and some *Prepona.* However, because his observations contradicted the classification of Comstock (based on wing characters and male genitalia) his paper was rejected by several journals upon the advice of reviewers (A. H. B. Rydon, pers. comm.). Much later, 1971, Rydon's paper found its way into a less widely read publication. In this example two evident sources of characters proved important in contradicting generally assumed "truths" about the classification of a group.

## Summary and Recommendations

We selected four areas for discussion of the proposals of Ehrlich and

Murphy: the problem of appropriate arbitration, the utility of pluralism in systematic and biogeographical theory, the intercontinental nature of kinship groups, and potential practical problems. These were derived from a careful reading of their critique and commentary on Miller and Brown (*loc. cit.*) and have, we hope, enlarged the context in which the various aspects of the controversy outlined by the Ehrlich and Murphy commentary can be considered by lepidopterists, both professional and amateur. Our criticisms are aimed more at the scientific implications of Ehrlich and Murphy's proposals than at judging the worthiness of their intentions. Many of their comments include generalizations with which many systematists would agree. Specific interpretation of these points, however, leads to inevitable problems which cannot be settled arbitrarily, we think, without undue problems for scientific study in the Lepidoptera. Although current divisiveness regarding nomenclature is unfortuante, the only background upon which any arbitration could take place would be one consistent with the current breadth of scientific pursuits in systematics and biogeography. Consideration of the complexity and theoretical variance in current approaches indicates a common ground for such arbitration is probably not possible. The fact of this complexity and variance, therefore, most likely inhibits value in the kinds of proposals suggested by Ehrlich and Murphy.

Ehrlich and Murphy are to be commended for bringing to the lepidopterists' community a touchstone for discussing current problems of taxonomy in the North American butterflies. Such discussion of the problems regarding scientific study of the North American fauna, especially in context with current approaches in systematic and biogeographic theory, should continue and is relevant to appreciating the historical contribution made by the thorough research provided in Miller and Brown's recent checklist. Journals in the field of Lepidoptera study should devote more emphasis to direct exchange of scientific and theoretical views among researchers. This would not only enhance the quality of work in Lepidoptera systematics but its reputation among systematists and biogeographers.

*Acknowledgments.* We are grateful to the following colleagues who read drafts of this manuscript and suggested directions for discussion and relevant changes and revisions. Their advice has helped clarify our considerations and concerns: Frederick H. Rindge and Randall T. Schuh (Dept. of Entomology, American Museum of Natural History), James E. Miller (Dept. of Entomology, Cornell University), Henri Descimon (Laboratory of Zoology, University of Marseilles), and Michael Schwartz (Dept. of Biology, City University of New York). We are also grateful to R. H. T. Mattoni, editor of *The Journal of Research on the Lepidoptera* for encouraging this contribution and maintaining correspondence with all of us during its preparation.

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## Editor's Note

The above paper by Johnson and Quinter is a comment on the papers of Ehrlich & Murphy and Miller & Brown regarding the recent *Catalogue/Checklist of the Butterflies of America north of Mexico* of the latter authors. Although discussion papers such as this are not usually refereed here, two major points appear in order. The first is the use of the word "kinship" to denote a potpourri of meanings, including "natural groupings", "phylogenetic relationship", "nature of relatedness", "similarity", and "clades". In biology (genetics) kinship correctly refers to the direct sharing of genes as in a genealogy, not properly in a phylogenetic context. The second point concerns the systematic analysis given in Table 2, data for which have not been generally available for critical consideration.

## Note

### Abnormal Chrysalis of *Papilio zelicaon* (Papilionidae)

The author has collected butterflies and moths in the Santa Barbara region for a quarter of a century, and during this long period of time has reared a number of endemic species. *Papilio zelicaon* (Lucas) is a common Swallowtail in this region and thousands of specimens have been reared to maturity over the years.

When raising such a great number of larvae of any one species, one naturally expects to obtain an occasional aberrant specimen. In the autumn of 1982 a couple hundred larvae of this species were raised, for later sale as pupae. One chrysalis of *Papilio zelicaon* was formed, and was recognized as being quite anomalous. The wings on one side of the pupae were fully developed, and totally absent on the other side (Fig. 1). If the butterfly had successfully emerged and spread its wings, we would have seen a freak specimen with normal wings on the left hand side, and no wings on the right hand side. Unfortunately, the insect died in the pupal stage. The chrysalis has been preserved in ethyl alcohol, and incorporated into my collection.

Fig. 1. **Upper**—normal side
**Middle**—wing missing
**Lower**—ventral view showing normal wing above and missing wing below

There is value in documenting such freaks in the journals of science. A good perspective on normalcy-abnormalcy in any given species is needed if we ever hope to unravel the underlying genetic reasons for such mistakes.

*Richard Carl Priestaf, 5631 Cielo Avenue, Goleta, CA 93017*

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COVER ILLUSTRATION: Integument sculpturing, 3rd instar larvae of *Lycaena epixanthe*. Scanning electron micrograph by David M. Wright from a forthcoming paper in Volume 22, Number 1.

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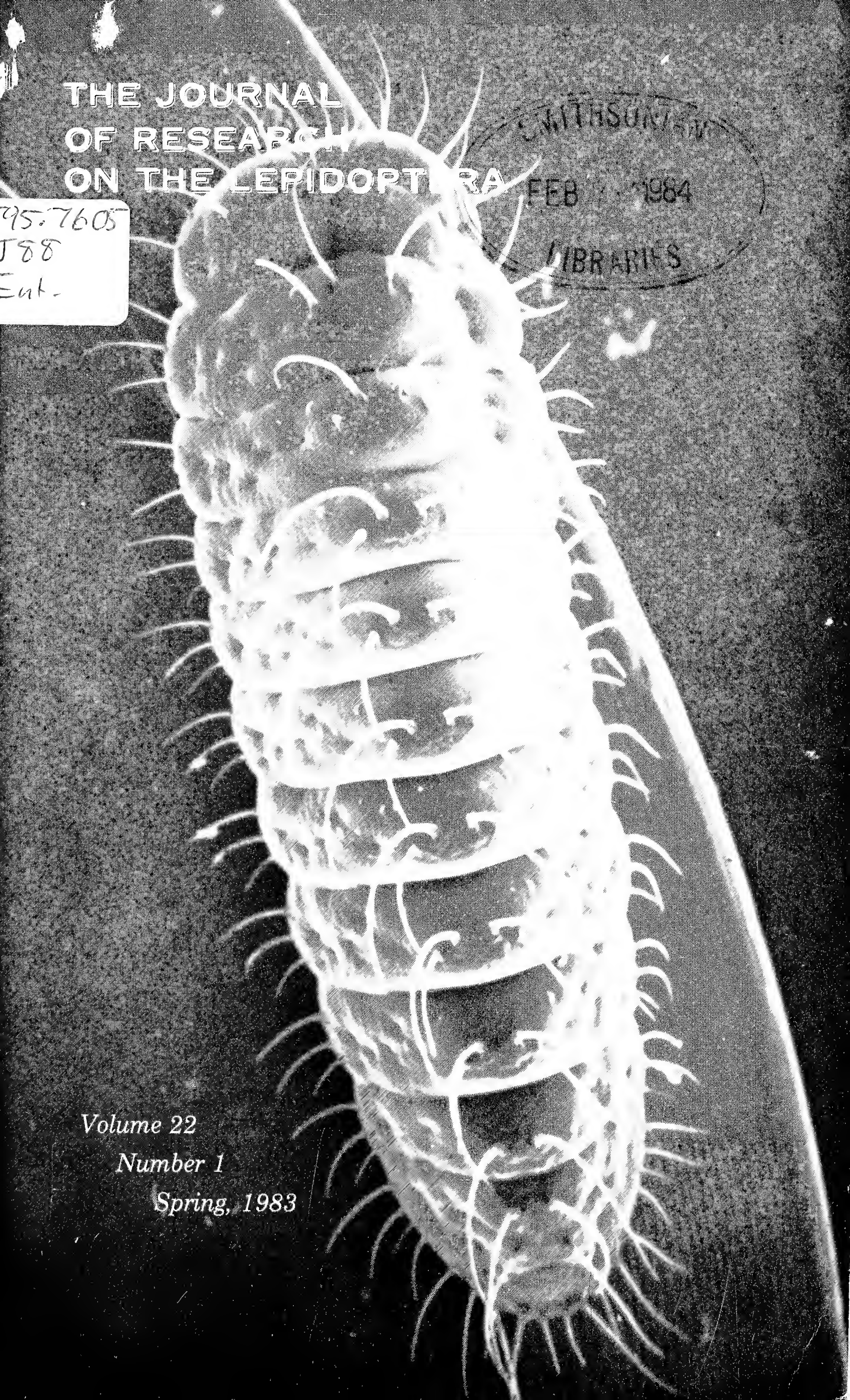

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# A Compilation of Data on Wing Homoeosis in Lepidoptera

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**Abstract.** On the basis of published records and unpublished material in various collections, 302 examples of fore/hindwing homoeosis and 31 examples of dorsal/ventral wing-surface homoeosis have been assembled from 16 families of Lepidoptera. In addition to the compilation of these records, individual cases have been characterized and the homoeotic mosaics have been mapped in a schematic format. Further, quantitative and statistical analyses of the various modes of appearance of homoeosis have been carried out as a basis for further studies on the mechanism of pattern formation in lepidopteran ontogeny.

## Introduction

A survey of wing homoeosis in Lepidoptera was published (Sibatani, 1980) in order to introduce to developmental biologists—with their rising interest in homoeosis—the wealth of reported data on this type of aberration. In that survey 161 cases already reported in the literature and three unrecorded cases of wing homoeosis in butterflies and moths were recorded.

Homoeosis is a morphological aberration of the animal body in which one part of the body is converted into another part. The examples of wing homoeosis I dealt with in that paper involve (a) the conversion of either a whole wing or part of the wing pattern on either surface of a wing into the corresponding structure of the wing on another thoracic segment, such as the conversion from fore to hindwing on one side of the host (F/H homoeosis), or (b) the conversion of part of the wing pattern on one surface of a wing into the corresponding part of the other surface of the same wing, such as occurs between the dorsal and ventral surfaces of either a fore or hindwing (D/V homoeosis).

In a continuation of this survey, data from more than 330 cases of wing homoeosis in Lepidoptera have been compiled, and are presented here in order that this information, hitherto recorded only in part be brought to the attention of lepidopterists. It is stressed that the principal aim of the communication is to gain more information into the nature of D/V homoeosis, to which *Drosophila*, the central subject of current studies on homoeosis, has so far contributed very little, but to which the Lepidoptera have contributed a sizable number of interesting examples (Sibatani, 1980).

## Materials and Methods

The cases of wing homoeosis dealt with in the previous report (Sibatani, 1980) included those compiled by Cockayne (1922, 1926, 1930) and Robertson (1969, 1977), recent reports of a lesser nature, and a few unrecorded specimens. In addition, I have now assembled more material, unrecorded and undescribed, from public and private collections, together with some recorded cases. The unrecorded material largely comes from the United Kingdom, the main source being the British Museum (Natural History) (BMNH) and the L. Christie collections.

The homoeotic specimens in the BMNH were in two sections, one the general collection of Lepidoptera from all over the world curated by Richard I. Vane-Wright, and the other, the collection of the British Lepidoptera, now under the curatorship of David J. Carter. Many of these specimens, all butterflies, had been set aside, as I understand by T. Graham Howarth, one of the disciples of the late Edward A. Cockayne and now retired from his service to the BMNH. Thus, in the collection of the British butterflies all the homoeotic specimens were grouped together and placed at the end of each species. This enabled me to work through them very efficiently within a relatively short period of time. The situation with moths was not so simple. Because of the sheer number of moths species from even the United Kingdom alone, and the apparent absence of a special cabinet for assembled homoeotic moths from other parts of the world, it has so far been impossible for me to assess all the homoeotic moths in the BMNH. I have therefore concentrated on only a few selected taxa of British moths.

L. Christie of London is a dedicated collector of homoeotic Lepidoptera, and his large collection, mostly butterflies, contains many good examples of wing homoeosis from the United Kingdom as well as from other parts of the world. Another remarkable source of material is an unpublished compilation o homoeotic specimens of *Luehdorfia* species (Papilionidae), all having bred in one year and mostly having arisen from a single local population in Japan (Masatoshi Nishimura, *in litt.*).

Altogether more than 330 cases were assembled. Most of the new material, as well as a significant fraction of the specimens reported in the literature, have now been examined directly or from good quality photographic records. Data were recorded and scored as in the previous report (Sibatani, 1980). Some of the descriptions made by Cockayne (1926, 1930) contain apparent inconsistencies in assignment of spaces between the veins: in some cases the space was called by the numeral used for the vein caudal to it (see *Papilio machaon* and "*Hyponephele*" *lycaon*—

Cockayne, 1926: pp. 216-217 and 222-223, respectively), but in other cases it was named according to the vein rostral to the space (see *Coenonympha pamphilus*—Cockayne, 1926: p. 222 and "*Pieris*" *davidis*—Cockayne, 1930: p. 219). I documented his descriptions with this point in mind, and was able to confirm my interpretation upon later examination of some of the specimens he described. Many cases reported by Cockayne, however, were not examined directly, as indicated in the following list which compiles the whole material used in this paper.

## List of Specimens with Wing Homoeosis in Lepidoptera

In this list edited versions of label data are given only when necessary for identification of individual specimens: they are given in full for so far unrecorded specimens, but only to a point needed to avoid an ambiguity arising from the nature of the reference to published data. In making this list, I have adopted the following policy and rules:

Usually, subspecies names are omitted. Personal collections are indicated by italicizing the collector's name in brackets. The following abbreviations are used throughout: A, P: anterior and posterior compartments; D, V, R, L, F, H: homoeotic mosaic(s) on dorsal, ventral surfaces; right, left wings; fore, hindwings respectively. Some data, of course, are insufficient and are only partially characterized in these terms. W: whole wing (or surface) homoeosis; BMNH: British Museum (Natural History), London; JSM: Japan Science Museum, Tokyo. *: illustrated; ( ▽ ): reference to an illustration is given; †: the specimen was examined by me; (†): original photographic reproduction of the specimen was examined. Years of the twentieth century for data (but not references) are given, wherever practicable, by the last two digits; years before 1900 are given in full.

## 1. Fore-/hindwing Homoeosis

### Adelidae

B1 *Adela viridella* Scopoli, Austria (?); Cockayne 1922: 13 WRH

### Zygaenidae

B2 *Zygaena occitanica* de Villers, France (?); Cockayne 1922: 13 (*) WRH

B3 *Zygaena exulans* Reiner & Hochenwarth, Europe (?); Cockayne 1922: 13 (*) WLH

B4 *Zygaena carniolica* Scopoli ♂ Austria; Cockayne 1922: 13 WLH

B5 *Zygaena filipendulae* Linnaeus, UK(?); Cockayne 1922: 13 (No. 2 of 2) WLF

B6 ____ [UK]; Cockayne 1926: 208 (Grosvenor)* WRH

B7 ____ [UK]; Cockayne 1922: 13 (Capper No. 1 of 2) WH

B8 *Zygaena lonicerae* Esper (or *Z. trioflii*?) UK; Cockayne 1922: 13; 1926: 208 WLH

B9 *Zygaena trifolii* Esper, UK(?); Cockayne 1922: 13 WLH

### Lasiocampidae

B10 *Dendrolimus pini* Linnaeus ♀ Germany(?); Cockayne 1930: 218 DRLH

B11 *Malacosoma castrensis* Linnaeus ♀ UK(?); Cockayne 1930: 218 DRH

### Hesperiidae

B12 *Hasora taminatus* Huebner, Philipines: Palawan iv.-v. 79 (*Sibatani*); Sibatani 1980: 3*† VRLF

### Papilionidae

B13 *Parnassius apollo* Linnaeus ♂ Austria; Cockayne 1922: 14 DRH

B14 ____ ♀ Austria; Cockayne 1922: 14 DLH

B15 *Pachliopta aristolochiae* Fabricius ♂ Burma: Maymyo 18 vii 71 Kinju Ikeda; Sibatani 1980: 3* JSM† VLF

B16 *Atrophaneura febanus* Fruhstorfer ♀ Taiwan *ex pupa* 6 viii 67 (*Shirozu*) (†) VRLF

B17 *Atrophaneura horishanus* Matsumura ♂ [Taiwan]; Cockayne 1923: 3 VLF

B18 *Papilio machaon* Linnaeus ♂ UK(?); Cockayne 1926: 216* DLF

B19 ____ [Russia]; Cockayne 1930: 213(*) DRF

B20 ____ Austria; Cockayne 1930: 213(*) DRF

B21 ____ ♀ UK: Norfolk Broads vi 36 L. W. Newman BMNH† DLH

B22 *Papilio polytes* Linnaeus ♀ Taiwan; Hayashi 1961: 97* DLF

B23 *Papilio memnon* Linnaeus ♀ Japan: Fukuoka (*Shirozu*) (†) DRF

B24 *Papilio maacki* Menetries ♀ Japan: Fukuoka *ex pupa* 23 vi 68 (*Shirozu*)(†) DLH

B25 ____ ♂ Japan; Hayashi 1961: 94* VRF

B26 *Papilio dialis* Leech ♂ Taiwan; Hama 1965* VLF

B27 *Papilio bianor* Cramer, China; Cockayne 1922: 14 VRH

B28 ____ ♀ Japan; Nishiyama & Hiuga 1975: 196* VLF

B29 *Papilio hoppo* Matsumura ♀ Taiwan; Ishizaki 1977*(†) VRH

B30 *Eurytides glaucolaus* Bates ♂ Columbia; Cockayne 1922: 14(*) VLF

B284-B302 *vide infra*

### Pieridae

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|---|---|
| B31 | *Delias hyparete* Linnaeus ♀ Burma: Maymyo vi 24 (*Christie*) † VRF |
| B32 | ____ ♂ India(?): K. Hills BMNH† VRF |
| B33 | *Delias belisama* Cramer ♂ Indonesia: Java, Goekaboemi iv 26 G. Overdijkink BMNH† VRH |
| B34 | *Aporia davidis* Oberthur (as *Pieris*) ♂ China; Cockayne 1930: 219* BMNH† VRH |
| B35 | *Pieris brassicae* Linnaeus ♀ UK; Frohawk 1938: 156* BMNH† VRH |
| B36 | ____ ♀ UK; Cockayne 1922: 14 VRH |
| B37 | *Pieris rapae* Linnaeus ♀ UK: Kent, Bexley bred Lot 78 L. W. Newman BMNH† VRH |
| B38 | ____ ♀ UK: 3rd brood bred 1. week x 31 Sutton (*Frohawk*) BMNH† VRH |
| B39 | *Pieris napi* Linnaeus ♂ UK: F. Green Lush 10 iv 32 (R. C. L. Perkins) BMNH† VRH |
| B40 | ____ ♂ Japan; Kuzuya 1969: 37* VRH |
| B41 | ____ ♀ UK: mixed parentage England × Ireland Anthony Thompson strain bred vii 49 (*Naomi Storer*) BMNH† VLH |
| B42 | ____ ♂ UK: Derry 1898 BMNH† VRLH |
| B43 | ____ ♀ UK: Dorset, Holcombe Wd. 16 vii 44 R. Troup (*Christie*) † VRF |
| B44 | ____ ♂ UK: Surrey, Hinchley Wood 21 iv 45 (*Christie*) † VRF |
| B45 | *Pieris melete* Menetries ♀ Japan; Kuzuya 1969: 38* DVRH |
| B46 | *Pontia daplidice* Linnaeus ♂ UK: Folkestone 11 viii 02 (*H. K. Smith*) BMNH† VLH |
| B47 | *Euchloe crameri romana* Calberla ♂ Italy: Ceri 30 km NWW of Rome 20 iv 80 (*Nakamura*)(†) VRF |
| B48 | *Anthocharis cardamines* Linnaeus ♂ UK: Petworth 6 vi 22 C. H. Cork (*Christie*) † VRF |
| B49 | ____ ♂ UK: Sandley 10 iv 45 (*H. B. Williams*) BMNH† VRF |
| B50 | ____ ♂ UK: Grassington (Grass Woods) W. Feather BMNH† VRF |
| B51 | ____ ♂ UK: Kent, Bexley v 41 L. T. Ford BMNH† VRF |
| B52 | ____ ♀ UK: Sussex, Loxwood bred *ex ovo* 27 iv 73 R. M. Craske BMNH† VLF |
| B53 | ____ ♂ UK: Herts., Tring 25 v 42 Goodson BMNH† VRF |
| B54 | ____ ♂ UK: Sussex, Loxwood bred *ex ovo* 23 iv 73 R. M. Craske BMNH† VRLF |
| B55 | ____ ♂ Japan; Fujisawa 1980* VLH |

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|---|---|
| B56 | ____ (as *Euchloe*) ♂ Europe(?); Cockayne 1926: 220* DLH |
| B57 | *Anthocharis belia* Linnaeus ♂ France: Perthus 20 iv 27 A. F. Pinhey (*Christie*)† DRH |
| B58 | *Colias hyale* Linnaeus ♀ UK: Birchington 30 ix 47 F. T. Vallins (*Howarth*)† VLF |
| B59 | ____ ♂ UK: Kent, Folkstone 21 viii-9 ix 1892 Colonel Le Grice (*Christie*)† DRF |
| B60 | *Colias erate* Esper ♂ China: Ting-Fu 1000 ft. vii 1889 A. E. Pratt BMNH† DLF |
| B61 | *Colias croceus* Geoffroy ♂ Europe(?) (*Christie*)† VRH |

**Lycaenidae**

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|---|---|
| B62 | *Eumaeus atala* Poey ♂ USA; Cockayne 1926: 220 VRF |
| B63 | *Thecla betulae* Linnaeus ♀ UK: Newton Abbot bred *ex ovo* vii 29 Perkins (*Christie*)† VLF |
| B64 | *Favonius cognatus* Staudinger ♂ Japan; Ishizaki 1976*(†) VLF |
| B65 | *Favonius orientalis* Murray ♂ Japan; Fujioka 1975: 54 (No. 37)* VLF |
| B66 | *Lycaena phlaeas* Linnaeus ♂ UK; Newman, 1959: 65* VLH |
| B67 | ____ ♀ UK; Robertson 1969: 88 (No. 11)* BMNH† VLH |
| B68 | ____ ♂ UK; Robertson 1969: 88 (No. 18)* VRH |
| B69 | ____ ♂ UK; Robertson 1977 (No. 3)* VRLH |
| B70 | ____ ♂ UK: Isle of Wight, Ventnor ?1965 D. H. Tress BMNH† VLH |
| B71 | ____ ♀ UK; Robertson 1969: 88 (No. 27)* VRLH |
| B72 | ____ ♂ UK: Near Devon 1881 (*Leech*) BMNH† VRH |
| B73 | ____ ♂ UK; Robertson 1969: 88 (No. 26)* VRLH |
| B74 | ____ ♂ UK; Robertson 1969: 88 (No. 24)* BMNH† VRLH |
| B75 | ____ ♂ UK; Robertson 1969: 87 (No. 2)* (*Christie*)† VLH |
| B76 | ____ ♀ UK: Hunts., Abbots Ripton 6 viii 28 W. Quibell (*Christie*)† VRH |
| B77 | ____ ♂ Eire: Cork viii 33 (*Christie*)† VLH |
| B78 | ____ ♂ UK; Robertson 1969: 88 (No. 20)* BMNH† VRLH |
| B79 | ____ ♀ [UK?]: Haar (or Haan?) 25 v 18 (*Christie*)† VRLH |
| B80 | ____ ♀ UK; Robertson 1969: 88 (No. 25)* VRLH |
| B81 | ____ ♂ UK; Robertson 1977 (No. 2)* VLH |
| B82 | ____ ♂ UK; Robertson 1977 (No. 1)* VRH |
| B83 | ____ ♀ UK; Robertson 1969: 88 (No. 17)* VRH |
| B84 | ____ ♀ UK; Robertson 1969: 88 (No. 19)* (*Christie*)† VRLH |
| B85 | ____ ♀ UK; Robertson 1969: 87 (No. 10)* VLH |
| B86 | ____ ♀ UK; Robertson 1969: 87 (No. 6)* VLH |
| B87 | ____ ♂ UK; Robertson 1969: 88 (No. 11)* VRH |
| B88 | ____ ♂ UK; Robertson 1969: 87 (No. 8)* VLH |

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| B89 | ____ ♀ UK; Robertson 1969: 87 (No. 9)* VLH |
| B90 | ____ ♂ UK; Robertson 1969: 88 (No. 14)* VRH |
| B91 | ____ ♂ UK; Robertson 1969: 87 (No. 7)* VLH |
| B92 | ____ ♂ UK; Robertson 1969: 88 (No. 13)* VRH |
| B93 | ____ ♀ UK; Robertson 1969: 88 (No. 16)* VRH |
| B94 | ____ ♀ UK; Robertson 1969: 88 (No. 15)* VRH |
| B95 | ____ ♀ UK; Robertson 1969: 88 (No. 21)* VRLH |
| B96 | ____ ♂ UK; Robertson 1969: 88 (No. 23)* VRLH |
| B97 | ____ ♂ Eire: Cork viii 33 (*Christie*)† VRH |
| B98 | ____ ♀ UK; Robertson 1969: 87 (No. 1)* VLH |
| B99 | ____ ♀ UK; Robertson 1969: 87 (No. 4)* VLH |
| B100 | ____ ♀ UK; Robertson 1969: 87 (No. 3)* VLH |
| B101 | ____ ♂ UK; Robertson 1969: 88 (No. 5)* VLH |
| B102 | ____ ♀ UK; Robertson 1969: 88 (No. 22)* VRLH |
| B103 | ____ ♀ UK; Robertson 1969: 88 (No. 28)* DRH |
| B104 | ____ ♂ UK(?): (*H. Symes*) bought 1970 (*Christie*)† VLF |
| B105 | *Lysandra coridon* Poda ♀ UK; Right & Leeds 1938: 86 (No. 131)* VRF |
| B106 | ____ (as *Agriades*) ♀ UK; Cockayne 1926: 219* BMNH† VRF |

**Nymphalidae**

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|---|---|
| B107 | *Mellicta athalia* Rottemburg ♂ UK: 19 P. M. Bright (*Stevens/Webb/Cockayne-Kettlewell*) BMNH† VLF |
| B108 | ____ (as *Melitaea*) ♂ UK; Cockayne 1926: 219 (No. 2 of W. Crocker) VRF |
| B109 | ____ ♀ UK: Essex 23 vi 37 B. J. L. (*Christie*)† VRF |
| B110 | ____ ♀ UK: Abbots Wood vi 1890 J. Slenny (*Christie*)† VRF |
| B111 | ____ ♀ UK: Belfairs Wood Southend 1936 C. P. Pickett, BMNH† VLF |
| B112 | ____ (as *Melitaea*) ♂ UK; Cockayne 1926: 219 (No. 1 of W. Crocker) BMNH† VRF |
| B113 | ____ ♂ UK: Kent, Blean vi 22 Lyon (*Christie*)† RLF |
| B114 | ____ ♀ UK: Blean 5 vii 31 BMNH† VRLF |
| B115 | ____ ♂ UK: Kent, Blean Woods vi 25 W. Crocker BMNH† VRLF |
| B116 | ____ ♂ UK: Blean Wood 24 vi 42 J. Shepherd (*Christie*)† VRF |
| B117 | ____ ♂ France: Gorge du Tarn 25 N. Malis (*Christie*)† VRLF |
| B118 | ____ ♂ UK: East Kent vi 21 L. W. Newman BMNH† VLF |
| B119 | ____ ♀ UK: near Canterbury 7 vii 33 H. Wood BMNH† VRF |
| B120 | ____ (as *Melitaea*) ♂ UK: Blean 4 vii 31 BMNH† VLF |
| B121 | ____ ♂ UK; Cockayne 1926: 218 (No. 3 of ♂♂)* BMNH† VLF |

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|---|---|
| B122 | ____ ♀ UK: Sussex 01 BMNH† VRF |
| B123 | ____ (as *Melitae*) ♂ UK; Cockayne 1926: 218 (No. 3 of 2♂♂)* BMNH† VRF |
| B124 | ____ ♀ UK: Canterbury bred vi 34 A & LB BMNH† VLF |
| B125 | ____ ♂ UK: Essex Hadleigh bred vi 33 A. F. Bowden BMNH† VRF |
| B126 | ____ ♂ UK: East Kent vi 19 BMNH† VLF |
| B127 | ____ ♂ UK: Blean Wood vii 35 Shepherd BMNH† (cf. B133) VLF |
| B128 | ____ ♂ UK: East Kent 17 vi 19 Willoughby Ellis BMNH† VRLF |
| B129 | ____ ♀ UK (*H. B. Williams*) BMNH† VLF |
| B130 | ____ ♂ UK: East Kent vii 31 (*Ellis*) BMNH† VLF |
| B131 | ____ ♂ UK: East Kent 27 vi 24 H. Wood (*Ellis*) BMNH† VRLF |
| B132 | ____ ♂ UK: Blean Wood 21 vi 30 H. K. Smith (*R. L. Ford*) BMNH† VRLF |
| B133 | ____ ♂ UK: Blean Wood vii 35 Shepherd (cf. B127) BMNH† VLF |
| B134 | ____ ♀ UK: (*Christie*)† VLF |
| B135 | ____ (as *Melitaea*) ♂ UK; Cockayne 1926: 218 (No. 1 of 3♂♂)* BMNH† VRLF |
| B136 | ____ (as *Melitaea*) ♀ UK; Cockayne 1930: 215* VRF |
| B137 | ____ (as *Melitaea*) ♀ UK; Cockayne 1930: 216 VLF |
| B138 | ____ ♂ UK: Kent, Blean Wood 26 vi 24 A. R. (*Christie*)† VRF |
| B139 | ____ ♂ UK: Kent, Blean vii 25 C. R. Verling-Brown (*Christie*)† VLF |
| B140 | ____ ♂ UK: Blean vi 34 P. A. Cardew (*Christie*)† VRF |
| B141 | ____ ♂ UK: Blean Wood vii 38 Shepherd BMNH† VLF |
| B142 | ____ ♂ UK: East Kent vii 1893 BMNH† VLF |
| B143 | ____ (as *Melitaea*) ♀ UK; Cockayne 1926: 219* BMNH† VRF |
| B144 | ____ ♀ UK: East Kent 21 L. W. Newman BMNH† VLF |
| B145 | ____ (as *Melitaea*) ♂ UK; Cockayne 1930: 216 (No. 1 of 3♂♂) VRF |
| B146 | ____ (as *Melitaea*) ♂ UK; Cockayne 1930: 216 (No. 2 of 3♂♂) VRF |
| B147 | ____ (as *Melitaea*) ♂ UK; Cockayne 1930: 216 (No. 3 of 3♂♂) VRF |
| B148 | ____ ♀ UK: Blean Wood 6 vii 36 J. N. Marcon BMNH† VRLF |
| B149 | ____ ♀ UK: Essex Hadleigh bred vi 33 A. F. Bowden BMNH† VLF |

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|---|---|
| B150 | ____ ♂ UK: Kent, Blean Wood vi 22 W. G. Nash BMNH† VLF |
| B151 | ____ ♂ UK: East Kent 23 vi 37 H. Wood BMNH† VLF |
| B152 | ____ (as *Melitaea*) ♂ UK; Cockayne 1930: 217 VRF |
| B153 | *Mellicta varia* Meyer-Duer (as *Melitaea*) ♀ Switzerland; Cockayne 1930: 217* BMNH† VRLF |
| B154 | *Melitaea cinxia* Linnaeus ♂ UK: Isle of Wight bred *ex larva* vi 45 E. W. Classey BMNH† VLF |
| B155 | ____ ♂ UK: Isle of Wight, St. Catherines 19 vii 24 C. R. Verling-Brown (*Christie*)† VRLF |
| B156 | ____ ♀ UK: Isle of Wight bred v 26 G. Watkinson BMNH† VRLF |
| B157 | ____ ♂ UK; Cockayne 1930: 217 (No. 1 of 2♂♂) VLF |
| B158 | ____ ♀ UK: Isle of Wight 10 BMNH† VRF |
| B159 | ____ ♂ UK: Niton 15 vi 10 BMNH† VRF |
| B160 | ____ ♀ UK; Cockayne 1930: 217 VRLF |
| B161 | ____ ♂ UK; Cockayne 1930: 217 (No. 2 of 2♂♂) VLF |
| B162 | ____ ♂ UK: Ventnor 24 vi 29 BMNH† VRLF |
| B163 | *Clossiana selene* Schiffermueller ♂ UK: Nevin 14 vi 30 W. Buckley BMNH† VLF |
| B164 | ____ (as *Brenthis*) ♂ Germany; Cockayne 1930: 215 VWRLF |
| B165-167 | ____ (as*Brenthis*) ♀♀ Germany; Cockayne 1930: 215(*) VWRLF |
| B168 | ____ ♂ UK: near Folkestone v 28 D. G. Marsh (*Christie*)† VLF |
| B169 | *Clossiana euphrosyne* Linnaeus ♂ UK: Braemar 5 vi 31 E. A. Cockayne BMNH† VLF |
| B170 | ____ (as *Brenthis*) ♀ UK; Cockayne 1930: 214* VWRF |
| B171 | *Argynnis paphia* Linnaeus ♂ UK: New Forest 14 vii 29 A. R. Hayward (*Christie*)† VRLF |
| B172 | ____ ♂ UK: near Tring 25 vii 42 A. T. Goodson BMNH† VRLF |
| B173 | ____ ♂ UK: New Forest 17 vii 19 D. C. Johnstone (*Christie*)† VRLF |
| B174 | ____ ♀ UK: Herts., near Tring 27 vii 41 A. L. Godson BMNH† VRLF |
| B175 | ____ ♀ UK: Somerset 17 vii 29 A. R. Hayward (*Christie*)† VRLF |
| B176 | *Fabriciana adippe* Schiffermueller ♀ UK: New Forestr bred vii 09 Ellis (*R. E. Ford*) BMNH† VRF |
| B177 | *Mesoacidalia aglaja* Linnaeus ♀ UK: Isle of Wight, Freshwater 27 vii 47 Goodson BMNH† VRF |
| B178 | *Inachis io* Linnaeus ♀ UK: Bexley bred 1937 (*Cockayne-Kettlewell*) BMNH† DLF |

B179 *Aglais urticae* Linnaeus ♀ UK; Ford 1945: 229*; Sibatani 1981* BMNH† VLF

B180 ____ UK; Cockayne 1930: 218* DRH

B181 ____ ♂ UK: North Kent bred vii 14 L. W. Newman (*Ellis/Ford*) BMNH† VLH

B182 ____ ♂ UK: North Kent ix 73 L. W. Newman BMNH† VRH

B183 ____ ♀ UK: W-D 1 ii 54 (*T. C. B. Craske/F. W. Frohawk*) (*Christie*)† VLH

B184 *Polygonia c-album* Linnaeus ♂ UK: Herts., Tring 14 ix 46 Goodson BMNH† VLF

B185 *Vanessa cardui* Linnaeus ♀ (*Christie*)† VRH

B186 ____ (as *Pyrameis*) ♂ India; Cockayne 1926 223* VLH

B187 *Vanessa indica* Herbst ♂ Japan; Hayashi 1961: 92* JSM† DLH

B188 *Vanessa atalanta* Linnaeus (as *Pyrameis*) ♂ UK; Cockayne 1926: 223* VLH

B189 *Precis orithya* Linnaeus ♀ Japan: Yayeyama *ex pupa* 3 viii 78 (*Shirozu*)(†) DLH

B190 *Precis oenone* Linnaeus (labelled as *Junonia delia*) ♂ Zimbabwe: Mashonaland, Umfuli R., Gadzema 4200 ft. BMNH† DLH

B191 *Neptis sappho* Pallas (as *N. aceris*) ♂ Japan; Hayashi 1961: 90 JSM† VLH

B192 *Bematistes poggei* Dewitz (labelled as f. *nelsoni*) ♀ [Africa] BMNH† VRH

B193 *Acraea eponina* Cramer (labelled as *A. terpsichore buxtoni*) ♀ South Africa: Umlali [Umhlali], Vumba ii 32; Sibatani 1980: 4* BMNH† VRH

**Satyridae**

B194 *Maniola jurtina* Linnaeus ♀ UK: Dover (*P. M. Bright*) Lot 30 at sale 3 xii 42 BMNH† VLF

B195 ____ (as *Epinephele*) ♀ UK; Cockayne 1930: 220 (No. 1 of 2♀♀) VLH

B196 ____ ♀ UK; Howarth 1973: pl. 4* VLH

B197 ____ ♂ UK: Herts., Tring 10 vii 48 Goodson BMNH† VLH

B198 ____ (as *Epinephele*) ♂ UK; Cockayne 1922: 15(*) VRH

B199 ____ (as *Epinephele*) ♀ UK; Cockayne 1930: 220 (No. 2 of 2♀♀) VRH

B200 ____ ♀ UK(?); "0/2/9/12" (*I. Matheson*) (*Christie*)† VLH

B201 *Hyponephele lycaon* Rottemburg ♀ France(?); Cockayne 1926: 222*; Sibatani 1980: 4* BMNH† VLH

B202 *Pyronia tithonus* Linnaeus ♂ UK; Russwurm 1978: pl. 40, fig. 3* VRH

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| B203 | *Erebia pandrose* Borkhausen (as *E. lappna)* ♀ Europe; Cockayne 1926: 223 (30 vi 12)* BMNH † VRH |
| B204 | ____ ♀ Europe; Cockayne 1926: 223 (28 vi 12)* BMNH† VRH |
| B205 | *Erebia aethiops* Esper (as ab. *derufata)* ♀ UK(?); Cockayne 1930: 220* VLH |
| B206 | *Coenonympha pamphilus* Linnaeus ♂ UK; Cockayne 1926: 220 (Hunts. 1891 or 1894)* VLH |
| B207 | ____ ♀ UK: Box Hill 10 vi 00 (*Christie)*† VRLH |
| B208 | ____ ♂ UK: Surrey, Chipstead 36 D. G. Marsh (*Christie)*† VRLH |
| B209 | ____ ♀ UK: Surrey 22 vi 20 T. Grosvenor (*Cockayne-Kettlewell*) BMNH† VRH |
| B210 | ____ ♂ UK; Cockayne 1926: 221 (Market Rasen No. 3) BMNH† VRH |
| B211 | ____ ♂ UK; Cockayne 1923: 2 (Kent) VLH |
| B212 | ____ ♂ UK: Sussex 12 vi 40 J. H. M. BMNH† VRH |
| B213 | ____ ♂ UK; Cockayne 1926: 221 (Market Rasen No. 1) BMNH† VRLH |
| B214 | ____ ♀ UK; Cockayne 1926: 222 VRH |
| B215 | ____ ♂ UK; Cockayne 1926: 222 ( Theydon Bois) VLH |
| B216 | ____ ♂ UK: Dorset, Hod Hill, Blandford vi 49 L. H. Newman BMNH† VRH |
| B217 | ____ ♂ UK; Cockayne 1926: 221 ( Market Rasen No. 2) BMNH† VRLH |
| B218 | ____ ♂ UK(?): Dondist 2 vi 49 (*Christie)*† VLH |
| B219 | ____ ♂ UK: Sussex, Eastbourne, Birling Gap 26 v 47 L. Christie (*Christie)*† VRH |
| B220 | ____ ♂ UK: Bucks., Chiltern Hills 27 v 19 G. B. Oliver (*H. B. Williams*) BMNH† VRLH |
| B221 | ____ ♀ UK: Belfairs Wood 23 vi 36 C. P. Pickett (*H. B. Williams*) BMNH† VRH |
| B222 | ____ ♂ UK: Sutton Colfield 17 vi 15 G. B. Oliver BMNH† VLH |
| B223 | ____ ♂ UK(?): Dondist 4 vi 49 (*Christie)*† VRLH |
| B224 | ____ ♂ UK: Sussex, Chipstead 31 v 24 F. W. Forhawk BMNH† VRH |
| B225 | ____ ♂ UK: Lewes 28 viii 31 L. A. E. Sabine (*H. B. Williams*) BMNH† VLH |
| B226 | ____ ♂ UK: Co. Clare vi 26 A. E. Sabine BMNH† VRH |
| B227 | ____ ♂ UK(?): (*Christie)*† VRH |
| B228 | ____ ♀ UK: New Forest 14 vi 31 C. King Smith BMNH† VRLH |
| B229 | ____ ♂ UK: Lincoln vi 27 W. Sperring BMNH† VLH |

| | |
|---|---|
| B230 | ____ ♀ UK; Cockayne 1923: 1 BMNH (but 17 vii 22) † VRH |
| B231 | ____ ♂ UK: Kent 18 vii 22 H. A. Leeds BMNH† VRH |
| B232 | ____ ♂ UK; Cockayne 1926: 221 (Grayshott v 15) BMNH† VRH |
| B233 | ____ ♀ UK: Bucks., Chilterns 19 G. B. Oliver (*H. B. Williams*) BMNH† VRH |
| B234 | ____ ♂ UK: Chiltern Hills vii 41 BMNH† VRH |
| B235 | ____ ♂ UK(?); Cockayne 1922: 15 (A. W. Mera)* VLH |
| B236 | ____ UK; Cockayne 1922: 14-15 (*Trans. Lond. N. H. Soc.* 1915) VLH |
| B237 | ____ UK; Cockayne 1922: 15 (Headley Common) VH |
| B238 | ____ UK; Cockayne 1922: 15 (*Maddison*) VLH |
| B239 | ____ ♂ UK: Gomshall S.G.C.R. 2 v 52 (*Castle-Russell/E. A. Cockayne*) BMNH† VRH |
| B240 | ____ ♀ UK: Herts. Royston 31 vii 30 BMNH† VLH |
| B241 | ____ ♂ UK: Kent(?), Lenham v 37 D. G. Marsh (*Christie*) † VRH |
| B242 | ____ ♂ UK: St. Osyth 18 vii 04 B. S. H. (*Christie*) † VRH |
| B243 | ____ ♀ UK: Surrey, Mitcham 5 ix 53 J. C. B. Craske (*Christie*) † VRF |
| B244 | ____ ♀ UK; Cockayne 1926: 220 BMNH† VRF |
| B245 | ____ ♂ UK; Cockayne 1923: 3 BMNH (but Monks Wood 7 v 22) † VRF |
| B246 | ____ ♀ UK: Somerset, Loxley Wood 15 vii 23 R. Troup (*Christie*) † VRF |
| B247 | ____ ♀ Eire: Sligo 20 vii 20 A. E. Sabine BMNH† VLF |
| B248 | *Coenonympha tullia* Mueller ♂ UK: Shropshire 23 vi 35 G. Greenwood BMNH† VRH |
| B249 | ____ ♀ UK: Perthsire (*Cockayne-Kettlewell*) BMNH† VRH |
| B250 | ____ (as *C. tiphon*) ♂ UK; Cockayne 1930: 219 BMNH† VRH |

**Danaidae**

| | |
|---|---|
| B251 | *Danaus chrysippus* Linnaeus ♀ South Africa: Johannesburg on loan from A. M. Altson BMNH† VLF |
| B252 | ____ (as f. *alcippus* Fabricius) ♀ Cameroon; Cockayne 1930: 213 DRF |

**Sphingidae**

| | |
|---|---|
| B253 | *Amorpha populi* Linnaeus, Europe(?); Cockayne 1930: 214 DRLF |

**Geometridae**

| | |
|---|---|
| B254 | *Eulithis prunata* Linnaeus (as *Cidaria*) ♂ UK; Cockayne 1923: 2 DRF |

| | |
|---|---|
| B255 | *Semiothisa (Macaria) notata* Linnaeus ♀ UK; Cockayne 1930: 218 DLH |

**Saturniidae**

| | |
|---|---|
| B256 | *Philosamia cynthia* Drury ♂ Europe(?); Cockayne 1930: 219 DRH |

**Noctuidae**

| | |
|---|---|
| B257 | *Bryoleuca domestica* Hufnagel (as *Bryophila perla*) UK; Cockayne 1930: 219(*) DLH |
| B258 | *Mamestra thalassina* Hufnagel, Germany; Cockayne 1922: 18 DLH |
| B259 | *Diarsia mendica* Fabricius (as *Noctua primulae*) ♂ UK; Cockayne 1926: 220 DLH |
| B260 | *Diarsia rubi* Vieweg (as *Noctua*) ♀ UK; Cockayne 1926: 220* DLH |
| B261 | *Noctua pronuba* Linnaeus ♂ UK: Sheringham 31 vii 57 P. R. Clarke BMNH† DRF |
| B262 | *Orthosia angulipennis* Matsumura ♀ Japan; Nakamura & Kishida 1976* DLH |
| B263 | *Orthosia gothica* Linnaeus (as *Taeniocampa*) ♂ UK; Cockayne 1922: 18* DLH |
| B264 | *Graphiphora augur* Fabricius ♂ UK: Dorking MV vi 58 R. F. Haynes (*Christie*) † DRH |
| B265 | *Tholera cespitis* Schiffermueller (as *Neuronia*) Europe(?); Cockayne 1922: 18(*) DRH |
| B266 | *Mythimna conigera* Schiffermueller (as *Leucania*) UK; Cockayne 1922: 18 DLH |
| B267 | *Xestia alpicola* Zetterstedt (as *Pachnobia hyperborea*) Europe(?); Cockayne 1922: 18 DLH |
| B268 | *Catocala nupta* Linnaeus ♂ UK; Cockayne 1926: 217* DRF |
| B269 | ____ UK(?); Cockayne 1922: 18 DRLF |
| B270 | ____ ♂ UK: Aldwick 14 viii 50 W. Minnion (*Christie*) † DLF |

**Arctiidae**

| | |
|---|---|
| B271 | *Arctia caja* Linnaeus UK; Cockayne 1922: 16 DLF |
| B272 | ____ UK; Cockayne 1922: 17 (No. 1 of 5 on p. 17) BMNH† DLH |
| B273 | ____ Europe (?); Cockayne 1922: 17 (No. 3 of 5) DRF |
| B274 | ____ Europe (?); Cockayne 1922: 17 (No. 4 of 5) DF |
| B275 | ____ ♀ UK; Cockayne 1922: 17(*) BMNH† DLF |
| B276 | ____ ♀ UK; Cockayne 1930: 214* BMNH† DRLF |
| B277 | ____ ♂ UK(?); Cockayne 1922: 17 (No. 2 of 5) BMNH† DRH |
| B278 | ____ ♂ UK: Bright (*Rothschild*) BMNH† DRLF |

| | |
|---|---|
| B279 | ____ ♀ French stock 15 iii 60 M. B. D. Nettlewell BMNH† DLF |
| B280 | ____ ♀ UK: Peterborough *ex larva* iv 31 F. W. Sharman BMNH† DVRH |
| B281 | ____ ♂ UK: Wicken 6 viii 37 W. H. A. Harris (*Cockayne-Kettlewell*) BMNH† DLH |
| B282 | ____ ♀ UK (*Howarth*)† DRLH |
| B283 | *Pericallia matronula* Linnaeus, Europe(?); Cockayne 1922: 17*(*) DRH |

## Addenda

### Papilionidae

| | |
|---|---|
| B284 | *Luehdorfia japonica* Leech ♂ Japan: Niigata-ken, Nishi-kambara-gun, Tsunodayama bred emrg. 4 iv 80 E. Yamazaki (Nishimura *in litt.* No. 4) (†) VRLF |
| B285 | ____ ♂ Japan: as above but 3 iv 80 (No. 3)(†) VRLF |
| B286 | ____ ♀ Japan: as above but 2 iv 80 (No. 12)(†) VRLF |
| B287 | ____ ♀ Japan: as above but 20 iii 80 (No. 14)(†) VRF |
| B288 | ____ ♂ Japan: as above but 16 iii 80 (No. 9)(†) VRLF |
| B289 | ____ ♂ Japan: as above but 4 iv 80 (No. 7)(†) VRLF |
| B290 | ____ ♂ Japan: as above but 2 iv 80 (No. 8)(†) VRLF |
| B291 | ____ ♂ Japan: as above but 3 iv 80 (No. 2)(†) VRLF |
| B292 | ____ ♀ Japan: as above but 4 iv 80 (No. 13)(†) VRLF |
| B293 | ____ ♀ Japan: as above but 29 iii 80 (No. 15)(†) VRF |
| B294 | ____ ♂ Japan: as above but 3 iv 80 (No. 1)(†) VRLF |
| B295 | ____ ♀ Japan: as above but 4 iv 80 (No. 11)(†) VRLF |
| B296 | ____ ♂ Japan: as above but 3 iv 80 (No. 6)(†) VLF |
| B297 | ____ ♂ Japan: Niigata-ken, Itoigawa-shi, Kotaki bred emerg. 16 iii 80 (Nishimura *in litt.* No. 16)(†) VRLF |
| B298 | ____ ♀ Japan: as in B284 but 3 iv 80 (No. 10)(†) VRF |
| B299 | ____ ♂ Japan: as above but 31 iii 80 (No. 5)(†) VRF |
| B300 | ____ ♂ Japan bred emerg. 14 iii 80 E. Yamazaki (Nishimura *in litt.* No. 18)(†) VLF |
| B301 | ____ ♀ Japan: Niigata-ken, Itoigawa-shi, Imai bred emerg. 3 iv 80 E. Yamazaki (Nishimura *in litt.* No. 17)(†) VRF |
| B302 | *Luehdorfia puziloi* Erschoff ♀ Japan: Nagano-ken, Omachi-shi,Inao bred emerg. 20 iii 80 E. Yamazaki (Nishimura *in litt.*)(†) VRLF |

## 2. Dorsal/Ventral Wing Homoeosis

### Hepialidae

| | |
|---|---|
| D1 | *Hepialus humuli* Linnaeus ♂ UK: Cockayne 1926: 226 VLH |

## Pieridae

D2 *Pieris napi* Linnaeus ♀ UK: New Forest vii 23 (*Christie*)† VRH
D3 ____ ♀ UK: Derry 1898 (*Salvage*) BMNH† VRLH
D4 ____ ♂ UK; Cockayne 1926: 226* BMNH† VLH
D5 ____ ♀ UK: Inverness, Forres bred 17 vii 10 (*Christie*) † VLH
D6 ____ ♂ UK: Cornwall, Bude bred 16 vii 08 (*Christie*) † VRLH
D7 *Colias croceus* Geoffroy ♀ BMNH† DRF

## Lycaenidae

D8 *Callophrys rubi* Linnaeus ♂ UK: Surrey, Headley 6 v 35 F. D. Coote (*Christie*) † VRF
D9 *Lycaena phaeas* Linnaeus ♀ UK: Near Herne Bay 23 v 20 D. G. Marsh (*Christie*) † VRF
D10 ____ ♀ UK; Robertson 1969: 89 (No. 37)* (*Christie*) † VRF
D11 ____ ♀ UK: Robertson 1969: 89 (No. 36)* (*Christie*) † VRF
D12 *Plebejus argus* Linnaeus UK; Cockayne 1923: 3 V
D13 ____ ♀ UK; Cockayne 1930: 220* DLF
D14 ____ ♀ UK; Cockayne 1926: 225 DLF
D15 ____ ♂ UK; Cockayne 1926: 225* BMNH† VRF
D16 ____ ♀ UK; Cockayne 1926: 226* DLH
D17 ____ ♀ UK; Cockayne 1930: 221 DRH
D18 ____ ♀ UK: Kent, Snodland 20 vii 28 D. G. Marsh (*Christie*) † DLH
D19 *Polyommatus icarus* Rottemburg ♂ UK: Aberdovey 23 vii 49 L. Birch (*Christie*) † VRLH
D20 ____ ♂ UK: Aberdovey 20 vi 49 L. Birch (*Christie*) † VRF/VLH
D21 ____ (as *Agriades thetis*) ♂ UK; Cockayne 1926: 224 VRF
D22 ____ (as *Agriades thetis*) UK; Pierce 1922 V
D23 *Lysandra coridon* Poda ♀ UK; Bright & Leeds 1938: 61* DLF
D24 ____ (as *Agriades* ♀ UK; Cockayne 1926: 225* DLF
D25 ____ (as *Agriades*) ♀ UK; Cockayne 1926: 227 VLH
D26 ____ ♀ UK; Bright & Leeds 1938: 86 VRH
D27 *Lysandra bellargus* Rottemburg ♂ UK: Folkstone ix 23 L. W. Newman (*Cockayne-Kettlewell*) BMNH† VRF

## Nymphalidae

D28 *Batesia hypochloros hemichrysa* Godman & Salvin ♀ Ecuador: Timotu BMNH† VRH
D29 *Vanessa cardui* Linnaeus (as *Pyrameis*) UK; Cockayne 1930: 221 VRLH

### Satyridae

D30 *Morpho terrestris* Butler (as *M. didius*) ♂ Peru; Cockayne 1926: 227* BMNH† VRH

D31 *Morpho menelaus* Linnaeus ♂ Cockayne 1926: 227 BMNH† VLH

## 3. Others

### Lycaenidae

A1 *Plebejus argus* Limmaeus ♂ UK: Kent 5 vii 33 H. A. Leeds (*Christie*)† VRH (partial duplication in mirror symmetry)

### Noctuidae

A2(=B257) *Bryoleuca domestica Hufnagel (as Bryophila perla)* Cockayne 1930: 219(*) DLH (F in reverse)

## Results and Discussion

*Geographic distribution of homoeotic specimens examined*

The specimens included in the list come from Europe, Africa, Asia and the Americas, whilst no single example of homoeotic Lepidoptera in the Australian region is known to me. An impressive majority derives from the United Kingdom, many of these having been duly reported by indigenous workers there. Next comes the contribution by the Japanese, both in reports and specimens. Although workers from both countries reported cases of exotic species, naturally most of the cases they recorded or assembled originated from their respective home countries. A curious fact is the absence of any record by the American workers. This has resulted in a conspicuous lacuna of known homoeotic specimens among American taxa. This fact of course need not mean that the American Lepidoptera are less prone, and that the British ones are more prone to produce wing homoeosis, but might simply reflect the characteristic attitudes of the lepidopterists of these countries.

*Taxonomic distribution of wing homoeoses in the sample*

Tables 1 to 3 summarize the number of samples in various taxa at three levels: families, genera and species. Again, they are subject to some human bias: (1) The range of individual higher taxa adopted here: Nymphalidae, including the acraeines, are separated from Danaidae and Satyridae, of which the last includes the morphines, a compromise suggested by Eliot (1978); *Pieris* and *Vanessa* are *sensu lato* whereas *Argynnis* is *sensu stricto*, hence a frequent occurrence of homoeosis among large fritillaries (B171-177) is not reflected in Table 3. (2) As noted before

(Sibatani, 1980), detection of wing homoeosis depends very largely on the type of wing patterning, that is, good markers which characteristically differ in the crucial areas of the wings subject to homoeotic conversion may or may not occur in various higher taxa. It is true that, as pointed out by previous workers (Cockayne, 1922, 1926, 1930; Robertson, 1969), individual taxa often exhibit characteristic trends in the mode and frequency of homoeosis detected on the wing. This point is clearly indicated in Table 4 in the case of F/H homoeosis (see the last four columns of this table).

Nevertheless, from overall wing patterning it would be expected that distribution of known homoeosis among four different wing surfaces need not be highly asymmetric. The possibility at least of detecting one type of homoeosis should be coupled with that of detecting a reciprocal case, the latter being as frequent. Hence, the taxonomic bias of the homoeosis seems to involve, at least partially, epigenetic biases characteristic of individual species, because most of these homoeoses are presumably produced through phenocopies rather than genetic mutations (see Sibatani, 1980).

### *Distribution of homoeoses among different wing surfaces*

The foregoing remarks clearly indicate that the overall figures on homoeosis of the entire Lepidoptera should involve biases due to the taxonomic and morphogenetic heterogeneity of the sample, genetic diversity and non-univorm artefact. Keeping this in mind, I will now analyse some spatially significant disparities in the frequency of homoeosis on the eight wing surfaces of specimens of different taxa.

With respect to the frequency of homoeosis, as controls I chose two near-trivial comparisons: the two sides of the wings and the two sexes. As expected, no significant differences were detected beteen right and left wings in the entire samples and individual taxa as shown in Tables 1, 2 and 4, except for F/H homoeoses in Pieridae, Satyridae and *Coenonympha* and for this I have no explanation.

With respect to sex, the frequency of F/H homoeosis was significantly higher for male than for female in *Anthocharis, Anthocharis cardamines, Mellicta-Melitaea*-complex, *Mellicta, Mellicta athalia, Coenonympha* and *Coenonympha pamphilus* as well as in the whole Lepidoptera.

Obviously, the picture was strongly influenced by the three species, *A. cardamines, M. athalia* and *C. pamphilus* with their significant sex bias and large sample sizes. It is conceivable that the sex difference was a real one in terms of the wing homoeosis either detected or produced; or it may be due simply to the fact that relatively more males than females could exist in collections of these three species. In *A. cardamines* in particular the conspicuous orange marker on the dorsal surface of forewing tip is male-specific.

Table 1. Fore/hindwing homoeosis in various families of Lepidoptera

| Taxon | Number of Cases Observed | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Total | Sex | | Wing | | | Surface (wing) | | Wing | | Surface | | Wing/surface affected | | | |
| | | ♂ | ♀ | L/R | L | R | Whole | Mosaic | F | H | D | V | FD | FV | HD | HV |
| Adelidae | 1 | | | | | 1 | (1) | | | 1 | | | | | | |
| Zygaenidae | 8 | 1 | | | 6 | 2 | (8) | | 1 | 7 | | | | | | |
| Lasiocampidae | 2 | | 2 | 1 | | 1 | | 2 | | 2 | 2 | | | | 2 | |
| Sphingidae | 1 | | | 1 | | | | 1 | 1 | | 1 | | | | | |
| Geometridae | 2 | 1 | 1 | | 1 | 1 | | 2 | 1 | 1 | 2 | | 1 | | 1 | |
| Saturniidae | 1 | 1 | | | | 1 | | 1 | | 1 | 1 | | | | 1 | |
| Noctuidae | 14 | 8 | 2 | 1 | 9 | 4 | | 14 | 4 | 10 | 14 | | 4 | | 10 | |
| Arctiidae | 13 | 3 | 5 | 4 | 5 | 3 | | 13 | 7 | 6 | 13 | 2 | 7 | 1 | 6 | 1 |
| Hesperiidae | 1 | | 1 | 1 | | | | 1 | 1 | | | 1 | | 1 | | |
| Papilionidae | 37 | 19 | 15 | 13 | 14 | 9 | | 37 | **32**······ | **5** | **8**···· | **28** | 5 | 27 | 3 | 1 |
| Pieridae | 31 | *21*····· | *10* | 3 | *8*····· | *20* | | 31 | 16 | 15 | **5**···· | **27** | 2 | 13 | 2 | 14 |
| Lycaenidae | 45 | 23 | 22 | 10 | 19 | 16 | | 45 | **7**····· | **38** | **1**···· | **44** | | 7 | 1 | 37 |
| Nymphalidae | 87 | 52 | 34 | 22 | 37 | 28 | 5 | 82 | **74**····· | **13** | **5**···· | **82** | 1 | 73 | 4 | 9 |
| Satyridae | 57 | 31 | 22 | 7 | **12**···· | **30** | | 57 | **6**····· | **51** | **0**···· | **57** | | 6 | | 51 |
| Danaidae | 2 | | 2 | | 1 | 1 | | 2 | 2 | | 1 | 1 | 1 | 1 | | |
| Total | 302 | **160**··· | **116** | 63 | 112 | 117 | 5(9) | 288 | 152 | 150 | **53**··· | **242** | 22 | 129 | 30 | 113 |

Pairs of figures connected by dots have statistically significant differences between them at $P < 0.05$ (italics) and $P < 0.01$ (bold prints) on $\chi^2$ tests. For abbreviations see the list in text.

Table 2. Wing homoeosis involving dorsal/ventral-surface conversion in various families of Lepidoptera

| | Number of Cases Observed | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Total | Sex | | Wing | | | Surface | | Wing | | Surface | | Wing/surface affected | | | |
| **Taxon** | | ♂ | ♀ | L/R | L | R | Whole | Mosaic | F | H | D | V | FD | FV | HD | HV |
| Hepialidae | 1 | 1 | | | 1 | | 0 | 1 | | 1 | | 1 | | | | 1 |
| Pieridae | 6 | 2 | 4 | 2 | 2 | 2 | 0 | 6 | 1 | 5 | 1 | 5 | 1 | | | 5 |
| Lycaenidae | 20 | 7 | 11 | 1 | 8 | 10 | 0 | 20 | 12 | 7 | 7 | 13 | 5 | 7 | 2 | 9 |
| Nymphalidae | 2 | | 1 | 1 | | 1 | 0 | 2 | | 2 | | 2 | | | | 2 |
| Satyridae | 2 | 2 | | | 1 | 1 | 0 | 2 | | 2 | | 2 | | | | 2 |
| Total | 31 | 12 | 16 | 4 | 12 | 14 | 0 | 31 | 13 | 17 | **8·····** | **23** | 6 | 7 | 2 | 19 |

For abbreviations and statistical analyses see Table 1.

Table 3. Lepidopteran taxa contributing more than one case of wing homoeosis to the present compilation.

| Family | Genus | No. of Species | | Species | No. of Cases | |
|---|---|---|---|---|---|---|
| | | F/H | D/V | | F/H | D/V |
| Zygaenidae | *Zygaena* | 6* | | *Z. filipendulae* | 3* | |
| Papilionidae | | | | *Parnassius apollo* | 2 | |
| | *Luehdorfia* | 2 | | *L. japonica* | 18 | |
| | *Papilio* | 7 | | *P. machaon* | 4 | |
| | | | | *P. maacki* | 2 | |
| | | | | *P. bianor* | 2 | |
| Pieridae | *Delias* | 2 | | *D. hyparete* | 2 | |
| | *Pieris* | 4 | | *P. brassicae* | 2 | |
| | | | | *P. rapae* | 2 | |
| | | | | *P. napi* | 6 | 5 |
| | *Anthocharis* | 2 | | *A. cardamines* | 9 | |
| | *Colias* | 3 | | *C. hyale* | 2 | |
| | | | | *C. croceus* | 1 | 1 |
| Lycaenidae | *Favonius* | 2 | | | | |
| | | | | *Lycaena phaleas* | 39 | 3 |
| | | | | *Plebejus argus* | | 7 |
| | | | | *Polyommatus icarus* | | 4 |
| | *Lysandra* | 1 | 2 | *L. coridon* | 2 | 4 |
| Nymphalidae | *Mellicta* | 2 | | *M. athalia* | 46 | |
| | | | | *Melitaea cinxia* | 9 | |
| | *Clossiana* | 2 | | *C. selene* | 6 | |
| | | | | *C. euphrosyne* | 2 | |
| | | | | *Argynnis paphia* | 5 | |
| | *Vanessa* | 3 | 1 | *V. cardui* | 2 | 1 |
| | | | | *Aglais urticae* | 6 | |
| | *Precis* | 2 | | | | |
| Satyridae | | | | *Maniola jurtina* | 7 | |
| | *Erebia* | 2 | | *E. pandrose* | 2 | |
| | *Coenonympha* | 2 | | *C. pamphilus* | 42 | |
| | | | | *C. tullia* | 3 | |
| | *Morpho* | | 2 | | | |
| Danaidae | | | | *Danaus chrysippus* | 2 | |
| Noctuidae | *Diarsia* | 2 | | | | |
| | *Orthosia* | 2 | | | | |
| | | | | *Catocala nupta* | 3 | |
| Arctiidae | | | | *Arctia caja* | 12 | |

*Whole wing homoeosis. Others are all mosaics within a single wing.

Table 4. Wing homoeosis in individual lower taxa

| Taxon | Type of Homoeosis | Total | Number of Cases Observed |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  | Sex |  | Wing |  |  | Surface |  | Wing |  | Surface |  | Wing/Surface Affected |  |  |  |
|  |  |  | ♂ | ♀ | L/R | L | R | Whole | Mosaic | F | H | D | V | FD | FV | HD | HV |
| *Luehdorfia* (Papilion.) | F/H | 19 | 11 | 8 | 12 | 4 | 3 | 0 | 19 | **19·····** | **0** | **0···** | **19** | 0 | 19 | 0 | 0 |
| *Luehdorfia japonica* | F/H | 18 | 11 | 7 | 11 | 4 | 3 | 0 | 18 | **18····** | **0** | **0···** | **18** | 0 | 18 | 0 | 0 |
| *Pieris* (Pieridae) | F/H | 11 | 4 | 7 | 2 | 1 | 8 | 0 | 11 | *2····* | *9* | *2···* | *10** | 0 | 2 | 1 | 9 |
| *Pieris napi* | F/H | 6 | 4 | 2 | 1 | 1 | 4 | 0 | 6 | 2 | 4 | 2 | 4 | 0 | 2 | 1 | 3 |
| *Anthocharis* (Pieridae) | F/H | 10 | *9····* | *1* | 1 | 4 | 5 | 0 | 10 | 2 | 8 | 8 | 2 | 0 | 7 | 2 | 1 |
| *A. cardamines* | F/H | 9 | *8····* | *1* | 1 | 3 | 5 | 0 | 9 | *1····* | *8* | 7 | 2 | 0 | 7 | 1 | 1 |
| *Lycaena phlaeas* (Lyc.) | F/H | 39 | 20 | 19 | 10 | 16 | 12 | 0 | 39 | **1···** | **38** | **1···** | **38** | 0 | 1 | 1 | 37 |
| *Mellicta+Melitaea* (Nym.) | F/H | 56 | *37····* | *19* | 13 | 23 | 20 | 0 | 56 | **56····** | **0** | **0···** | **56** | 0 | 56 | 0 | 0 |
| *Mellicta* | F/H | 47 | *31····* | *16* | 9 | 20 | 18 | 0 | 47 | **47····** | **0** | **0···** | **47** | 0 | 47 | 0 | 0 |
| *Mellicta athalia* | F/H | 46 | *31····* | *15* | 8 | 20 | 18 | 0 | 46 | **46····** | **0** | **0···** | **46** | 0 | 46 | 0 | 0 |
| *Argynnini* (Nym.) | F/H | 15 | 7 | 8 | 9 | 3 | 3 | 5 | 10 | **15····** | **0** | **0···** | **15** | 0 | 15 | 0 | 0 |
| *Clossiana* (Nym.) | F/H | 8 | 4 | 4 | 4 | 3 | 1 | 5 | 3 | **8····** | **0** | **0····** | **8** | 0 | 0 | 8 | 0 |
| *Coenonymnpha* (Saty.) | F/H | 45 | *28···* | *13* | 7 | *12····* | *25* | 0 | 45 | **5···** | **40** | **0···** | **45** | 0 | 5 | 0 | 40 |
| *Coenonympha pamphilus* | F/H | 42 | *26···* | *12* | 7 | 12 | 22 | 0 | 42 | **5···** | **37** | **0···** | **42** | 0 | 5 | 0 | 37 |
| *Arctia caja* (Arctiidae) | F/H | 12 | 3 | 5 | 4 | 5 | 2 | 0 | 12 | 7 | 5 | *12·····* | *1** | 7 | 0 | 5 | 1 |
| *Pieris napi* (Pieridae) | D/V | 5 | 2 | 3 | 2 | 2 | 1 | 0 | 5 | *0·····* | *5* | *0·····* | *5* | 0 | 0 | 0 | 5 |
| *Lycaena phlaeas* (Lyc.) | D/V | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 |
| *Plebejus argus* (Lyc.) | D/V | 7 | 2 | 4 | 0 | 4 | 2 | 0 | 7 | 3 | 3 | 5 | 2 | 2 | 1 | 3 | 0 |

For abbreviations and statistical analyses see Table 1. Figures with an asterisk indicate cases where homoeosis appears on both surfaces of a wing.

Concerning the mosaicism in wing homoeosis, the results are clear-cut: the whole wing homoeosis is very predominant in Zygaenidae (although it appears exclusive in the list, several homoeotic mosaics can now be added—Sibatani, to be published); whole-surface homoeosis apears only in genus *Clossiana*. This point would certainly bear on the mechanism of homoeosis and of epigenetic control of wing morphology in these species.

Homoeosis is evenly distributed between fore and hindwing for the whole Lepidoptera, but this is deceptive because individual taxa in Tables 1 and 4 clearly show a strong tendency of F/H wing non-equivalence in individual species. Hence the tendency towards fore- or hindwing homoeosis is more species-specific, and as stated above, cannot be solely ascribed to the presence of favourable markers for detection.

Pooled data from the whole Lepidoptera indicate that the dominance of ventral surface over dorsal surface for homoeosis is quite conspicuous. Again, however, this was deceptive because such a trend is limited to butterflies, moths showing exactly the opposite trend. The forewing dorsal surface of moths and both fore and hindwing ventral surfaces of butterflies are the most homoeosis-prone areas. This may be related to the exposed surface of the wing in the resting position of the insect. These parts of the wing tend to be marked more conspicuously and specifically than the other areas which remain unexposed in resting. The detection of homoeotic mosaics seems to be due to the existence of good markers. However, the tendency of individual taxa to show either F/H or D/V homoeosis is unidirectional, indicating that more than just ease of detection causes this bias. Epigenetic factors involved in the generation of homoeosis may well be evolutionarily related to the insect's behaviour in its resting position.

### *Topography of homoeosis within a wing surface*

Figures 1-12 are a schematic mapping of homoeotic mosaics for all the specimens in which I could locate the position of mosaics with a certain degree of accuracy (see Sibatani, 1980 for definition of accuracy). In so doing, I had to resort to one kind of topological anisomorphism regarding the wing base, where anal (A) and subconstal (Sc) veins, and discal and other spaces flanking them meet. Hence the proximal end of the wing spaces including the discal space should be mapped as a point. In my scheme however it is mapped diffusely along a line, and in the case of discal space, on a very long line, thus enormously inflating the relative area of the mosaics proximad, just as in the case of Mercator's projection of the two poles of the Earth on a two-dimensional map. However, the objective of this mapping is to indicate position and boundary of mosaics relative to individual spaces and veins, and the mentioned anisomorphism does not affect this point.

As already pointed out (Sibatani, 1980), the mosaics of F/H homoeosis tend to occur most frequently in the posterior half of the wing, the boundary of the anterior and posterior halves occurring somewhere in space $M_1$-$M_2$. I regard these halves as equivalents of anterior and posterior compartments in *Drosophila melanogaster* Meigen (Crick and Lawrence, 1975; see Sibatani, 1980 for discussion and further references).

This point can be seen easily from Figures 1-11 illustrating F/H homoeotic mosaics. However, the same is not true with the D/V homoeosis; indeed, even the reverse is sometimes true (Fig. 12). A comparison of the topography for the two types of homoeosis is made in Figure 13, which corresponds to Figure 4 of Sibatani (1980) but which has been revised on the basis of the new data presented in this paper.

Analysis of cases where F/H homoeotic mosaics occurred in the anterior half of the wing is given in Table 5. On the dorsal surface, the homoeotic mosaic appeared in the anterior half of both wings at fairly high frequencies, but the corresponding events were much rarer on the ventral surface. The mosaic was seldom confined to the anterior half of the wing, the majority of these cases exhibiting mosaics in both anterior and posterior halves. Most of these mosaics are discontinuous at the boundary of the putative anterior and posterior compartments, and only a small number of cases exhibited a homoeotic patch lying across the boundary line. The low frequency of such cases is compatible with the assumption that they represent confluent clones arising independently in the two halves of the wing. Although the D/V homoeosis appeared more frequently in the anterior half of the wing (see Fig. 12), there is only one example (D23 *Lysandra coridon*, on forewing dorsal surface) out of a total of 31 cases, all wings and surfaces inclusive, showing a homoeotic patch continuous between the two halves of the wing. Hence I do not consider that these "confluent" homoeotic patches constitute sufficient evidence to negate the assumption that lepidopteran wings can be divided into anterior and posterior compartments (Sibatani, 1980).

### *Multiple occurrence of homoeotic mosaics*

The above assumption implies that homoeotic mosaics generally represent clones of epigenetically homoeotic cells. Although surely some clones may have been split into some discrete patches, we may assume that the majority of the multiple homoeotic mosaics found in my samples are of independent origin in an individual subject to some homoeotic predisposition (phenocopy). If this is so, the bilateral occurrence of homoeotic patches on either surface of the forewings or hindwings and the multiple occurrence of homoeotic mosaics on the same surface of only one of the paired wings basically represent the same phenomenon. I had a chance to test this hypothesis with a population of *Luehdorfia japonica* having a rather high incidence of homoeotic modification (B284-B301).

These homoeotic specimens were found amongst some 1,550 specimens reared in several batches from a limited area on the mid-northern slope of Honshu, Japan, in one year (season). Small homoeotic mosaics appeared on the ventral surface of either or both forewings in each of 18 specimens. The right and left wings were pooled and the frequency of the cases exhibiting various numbers of homoeotic patches on a wing was scored (Table 6). The distribution of the mosaics conformed to the Poisson distribution in the homoeotically predisposed specimens but strongly deviated from it in the total population. The results are thus compatible with the assumption that the homoeotic mosaics would appear randomly on the homoeosis-prone surface of either of the bilateral wings in individuals subject to some homoeosis-inducing agent.

*Trends in individual taxa*

Quite apart from the tendency of individual taxa to generate detectable

Table 5. Homoeotic mosaics occurring in the putative anterior compartment of the wings in Lepidoptera

| | **Forewing** | | **Hindwing** | |
|---|---|---|---|---|
| | **Dorsal** | **Ventral** | **Dorsal** | **Ventral** |
| Total number of homoeotic wings examined | 18 | 147 | 26 | 131 |
| Number of wings with homoeotic mosaics occurring in the anterior half of the wing | | | | |
| Group 1* | 11 | 6-7 | 8-10 | 5-6 |
| Group 2** | 10 | 6-7 | 5-7 | 4-5 |
| Group 3*** | (1) | 1 | 2-4 | 1(2) |
| Percent of total | | | | |
| Group 1 | 0.61 | 0.04-0.05 | 0.31-0.38 | 0.04-0.05 |
| Group 2 | 0.56 | 0.04-0.05 | 0.19-0.27 | 0.03-0.04 |
| Group 3 | (0.06) | 0.01 | 0.08-0.15 | 0.01(0.02) |

*Cases in which any homoeotic mosiacs occurred on or rostral of $M_1$. The higher figures include cases where homoeosis did not extend rostrad beyond veing $M_1$.

** Cases where homoeotic mosaic occurred on both sides of the putative compartment boundary somewhere in space $M_1$-$M_2$. Higher figures as in Group 1.

***Cases where a homoeotic mosaic occurred, which lay astride the putative boundary, thus solidly connecting homoeotic patches which extended rostrad of $M_1$ and caudad of $M_2$. Figures in parentheses represent some ambiguous cases without clearly defined mosaic outlines in my records. These cases comprised the following specimens, the taxa in parentheses corresponding to the figures in parentheses: FD, (B252 *Danaus chrysippus*); FV, B104 *Lysandra coridon*; HD, B264 *Graphiphora augur*, B283 *Pericallia matronula*, B103 *Lycaena phlaeas*, B180 *Aglais urticae*; HV, B196 *Maniola jurtina*, (B202 *Pyronia tithonus*).

Table 6. Frequency of isolated homoeotic patches on the forewing in a population of *Luehdorfia japnica.*

| | **Number of Homoeotic Wings Found** | |
|---|---|---|
| **Number of Homoeotic Patches on a Wing** | **In a whole population examined** | **Among specimens carrying homoeosis** |
| 0 | 3072* | 8 |
| 1 | 15 | 15 |
| 2 | 9 | 9 |
| 3 | 3 | 3 |
| 4 | 0 | 0 |
| 5 | 1 | 1 |
| **Total** | 3100* | 36 |
| $P$** | <0.005 | >0.75 |

*Based on a rough estimation.

**$\chi^2$ test for a significant deviation from Poisson distribution.

homoeosis on a particular wing surface, which may be partially related to the characteristic patterning of the taxon, there are other trends in the appearance of homoeosis in individual taxa. Variables involved are frequency and degree of mosaicism and propensity for general bilateral mosaicism.

Table 4 lists some of the taxa showing a higher frequency of wing homoeosis. In the descending order of number of cases examined at the species level, they include *Mellicta athalia, Coenonympha pamphilus, Lycaena phlaeas, Luehdorfia japonica, Arctia caja, Anthocharis cardamines* and *Pieris napi* for F/H homoeosis, and *Plebejus argus, Pieris napi* and *Lycaena phlaeas* for D/V homoeosis. In the genera of *Mellicta, Melitaea* and the arginine group including *Argynnis, Mesoacidalia* and *Fabriciana* as well as in *Luehdorfia,* the mosaics tend to appear in small patches, often in large numbers and also on both wings (Figs. 4, 7-9, 14). In *Arctia caja* (plus one case of *Pericallia matronula* belonging to the same family Arctiidae) the mosaics were larger but occurred frequently widespread in multiple patches on the dorsal (but sometimes even on the ventral) surface of both wings. In *Lycaena,* the F/W homoeosis tends to appear on the ventral hindwing, whereas the D/V homoeosis, albeit so far known only in small number, appears on the ventral forewing, though other modes of appearance should have been recognized as easily. Also noteworthy is the fact that no D/V homoeosis has been known in males of *Favonius, Neozephyrus* and *Chrysozephyrus* of the same family (Lycaenidae) with their green dorsal surfaces very distinct from the grey or brown ventral surfaces. In view of the fact that these taxa are very much sought after by collectors in Japan, the D/V homoeoses appear more readily in some species of *Lycaena* and *Plebejus* than in the thecline genera including the above and the English or European *Quercusia quercus*, in which detection of a D/V homoeosis would also be easy.

Further, no homoeosis in *Melitaea, Mellicta*, argynnine genera, *Plebejus* and *Lycaena* have been reported from Japan, although they are rather common in that country whence a number of wing homoeoses in Lepidoptera has been reported. This suggests that the same or related species in different countries may not display comparable propensity for wing homoeosis.

### *D/V homoeosis*

I wish to discuss this subject in a separate paper addressed to developmental biologists (but see Figs. 15-17 in this paper). However, I should point out that two of the three D/V homoeoses I record here of *Lycaena phlaeas* (D10 and D11) are those described by Robertson (1969) as heteromorphosis rather than homoeosis, a treatment which I followed previously (Sibatani, 1980). However, reexamination of these specimens has now revealed that not only the golden orange ground colour but also black spots on the discal areas of the forewing dorsal surface appear on the ventral surface of the same wing, the latter being superimposed on the black spots on the ventral surface, which are slightly smaller than the corresponding ones on the dorsal surface (compare left (normal) and right (homoeotic) forewings in Figs. 15 and 16). Hence I am now inclined to regard them as examples of true D/V homoeosis.

### *Structural modifications*

The homoeotic mosaics featuring the F/H wing pattern conversion does not usually entail a conversion of venation or wing shape. In the case of a complete conversion of the hindwing posterior half (compartment) ventral surface to the corresponding part of the forewing in B193 *Acraea eponina* (Sibatani, 1980), I have now ascertained that vein 3A which exists only in the hindwing is atrophied in the homoeotic wing carrying a forewing pattern on the ventral surface posterior half.

In the case of such extensive conversion of the posterior half of the wing occurring in a tailed papilionid taxon, there is some sign of change in the wing form: in B21 *Papilio machaon* (see Fig. 3, K) in which the dorsal surface of the most part of the posterior half of the left hindwing is converted into the corresponding forewing part, the tail, or the extension of vein $M_3$, on the hindwing is truncated but fringed, showing that it was not broken off. A corresponding reverse case (B18 *P. machaon*, see Fig. 3, D), the allotypic (= homoeotic) $M_3$ on the forewing exhibits only a slight protrusion (see Cockayne, 1926: pl. 62, fig. 3).

*Unusual cases*

There are a few unusual cases which deserve attention and probably careful study. There are two cases (B45 *Pieris melete* and B280 *Arctia caja*) in which both dorsal and ventral surfaces of one wing appear to have homoeotic mosaics. *P. melete* (Fig. 5, L) exhibits entirely different distributions of mosaic areas on the two surfaces of a hindwing, whereas *A. caja* (Fig. 2b) has mosaics on the corresponding areas of the dorsal and ventral surfaces of the wing. The authenticity of the homoeotic nature on the ventral surface of these examples would need further verification.

Further there is a unique example of D20 *Polyommatus icarus* where two entirely independent D/V homoeotic mosaics appeared on ventral surfaces of the right forewing and the left hindwing (Fig. 12, E, K). Apart from this, I examined two female specimens of this species (in the L. Christie collection) which exhibited blue areas on the ventral surface of a wing. But since the dorsal surface of these female specimens was dark rather than blue as in the male, those blue areas could not be held as a D/V homoeosis. This gives a warning to accepting blue scales resembling those of the dorsal surface of a male wing in most polyommatine taxa, when they appear on the ventral surface, as D/V homoeosis.

Finally, as mentioned before, genus *Clossiana* shows a high frequency of F/H homoeosis occurring on the whole wing surface which is rarely found in nature. I will discuss the whole wing conversion often observed in Zygaenidae in a separate article as a supplement to this paper, and in which I will also supply selected additional data having some remarkable implications.

Two unusual cases of duplication in reverse polarity were included in the list under the heading of "3. Others." One is illustrated here (Fig. 18). This specimen, A1 *Plebejus argus* has a normal dorsal surface pattern, but the ventral surface of its right hindwing exhibits a mirror-symmetry duplication in part, presumably covering the spaces between Rs and $M_3$. If the symmetry axis lies, as it appears, on vein $M_3$, it deviates slightly from the putative compartment boundary in mid space $M_1$-$M_2$. Moreover, there exists a complete complement of the posterior half of the wing, so that analogy to *engrailed* phenotype in *Drosophila* (Morata and Lawrence, 1976) in which the posterior compartments in meso- or metathorax are converted into a mirror image of the anterior compartment, does not hold. Hence it is doubtful that this represents a phenocopy of "engrailed"-type homoeosis.

Another example of mirror-symmetry duplication of a forewing, A2 *Bryoleuca domestica* has already been commented on (Sibatani, 1980).

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## Appendix: Glossary of some technical terms

*Compartment.* In the development of *Drosophila* from early embryo to early pupal stage, the prospective adult structures in the head, thorax and genitalia arise and grow in the form of imaginal discs. Descendants of a single cell in a developing imaginal disc can be identified in the adult if that cell has undergone a somatic chromosome recombination which converts the cell's genotype from the heterozygous to the homozygous state of a recessive gene affecting the adult's phenotype. Hence, the descendants of a cell, or the clone, may form a genetically labelled mosaic in the adult structure. Analysis of clones started at various stages of development has revealed that development of the imaginal disc proceeds through successive binary partitionings of the cell population of the disc into regions which will follow alternative developmental pathways. Such regions are compartments, their boundaries not usually being transgressed by the clones derived from those multiple cells which are founders of a compartment. For instance, parts of the wing and haltere discs are first allotted to the anterior and posterior compartments, and then each of them is further partitioned into the dorsal and ventral compartments, and so on.

*Epigenetic.* Adjective of 'epigenesis' which is an expression coined in the 18th century (hence preceding introduction of the word 'genetics') as a concept opposite to 'preformation'. With the introduction of the concept of 'epigenetics' (developmental biology as analysed in terms of unfolding gene functions during embryogenesis), the meaning of the word 'epigenetic' has recently been relaxed and expanded to cover the changes in genetic expression during development.

*Phenocopy.* Experimental analyses of *Drosophila* indicate that external agents, such as ether or heat shock, applied at some early crucial stage of development cause some mutant phenotypes to appear in individuals with wild-type genotype. Such a phenomenon is called the phenocopy.

Figs. 1-12. Maps of homoeotic mosaics in Lepidoptera wings. All the examined specimens are included herein as far as sufficient data were obtained by direct examination or through photographic records, description and/or illustration in the literature. Each surface of the wing is mapped by a horizontal array of quadrangles and a broad triangle, representing the intervenous and discal spaces, respectively, the vertical lines representing veins as indicated at the bottom of each column. Unusual abbreviations: c, costa; d, dorsum; A or 1A, 1A+2A; Cu, CuA; Sc, $Sc+R_1$. Homoeotic mosaics appearing on the dorsal and ventral wing surfaces and the left and right wings are all pooled, but they are distinguished by thick (U, dorsal surface; V, ventral surface) and thin (on the corresponding sides of the column) vertical lines, respectively. The broken vertical lines between $M_1$ and $M_2$ indicate the approximate position of the putative boundary of the anterior and posterior compartments. Numbers on the right (occasionally left) end of each horizontal array indicate identification numbers of the recorded specimens as compiled in the list on pp. 3-16; plain numbers refer to B series (F/H homoeosis). Those grouped together in a column with a number preceded by D at the bottom of the column all belong to the D series (D/V homoesis). Capital alphabet letters and single-brackets on the left indicate individual species as indexed in the legend. Black areas are homoeotic mosaics with definable boundaries; obliquely hatched areas are homoeotic areas whose boundaries are obscure in the available data; vertically hatched areas contain numerous small mosaics difficult to map. Stippled areas represent parts of the wing whose homoeotic nature is questionable or uncertain.

Figs. 1-11. F/H homoetic mosaics.

Fig. 1. Moths (except for Arctiidae) and some butterflies. (a), (c) and (d), forewings; (b) hindwings.

(a), Noctuidae—A, *Noctua pronuba* Linnaeus; B, *Catocala nupta* Linnaeus.

(b), Lasiocampidae, Geometridae, Saturniidae and Noctuidae—C, *Dendrolimus pini* Linnaeus; D, *Semiothisa (Macaria) notata* Linnaeus; E, *Philosamia cynthia* Drury; F, *Diarsia rubi* Vieweg; G, *Diarsia mendica* Fabricius; H, *Graphiphora augur* Fabricius; I, *Orthosia angulipennis* Matsumura; J, *Orthosia gothica* Linnaeus; K, *Tholera cespitis* Schiffermueller; L, *Mythimna conigera* Schiffermueller; M, *Xestia alpicola* Zetterstedt.

(c), Hesperiidae—N, *Hasora taminatus* Huebner.

(d), Lycaenidae—O, *Eumaeus atala* Poey; P, *Thecla betulae* Linnaeus; Q, *Favonius cognatus* Staudinger; R, *Favonius orientalis* Murray; S, *Lycaena phlaeas* Linnaeus; T, *Lysandra coridon* Poda.

Fig. 2. Arctiidae. (a), forewings—*Arctia caja* Linnaeus. (b), hindwings—A, *Pericallia matronula* Linnaeus; B, *Arctia caja* Linnaeus.

Fig. 3. Papilionidae. (a), forewings—A, *Pachliopta aristolochiae* Fabricius; B, *Atrophaneura febanus* Fruhstorfer; C, *Atrophaneura horishanus*

Matsumura; D, *Papilio machaon* Linnaeus; E, *Papilio memnon* Linnaeus; F, *Papilio polytes* Linnaeus; G, *Papilio maacki* Ménétriès; H, *Papilio dialis* Leech; I, *Papilio bianor* Cramer; J, *Eurytides glaucolaus* Bates.

(b), hindwings—K, *Papilio machaon* Linnaeus; L, *Papilio hoppo* Matsumura; M, *Papilio maacki* Ménètriès.

Fig. 4. *Luehdorfia* species (Papilionidae), forewings. (a) and (b) A, *L. japonica* Leech; (b) B, *L. puziloi* Erschoff.

Fig. 5. Pieridae. (a), forewings—A, *Delias hyparete* Linnaeus; B, *Pieris napi* Linnaeus; C, *Euchloe crameri romana* Calberla; D, *Anthocharis cardamines* Linnaeus; E, *Colias hyale* Linnaeus; F, *Colias erate* Esper.

(b), hindwings—G, *Aporia davidis* Oberthur; H, *Delias belisama* Cramer; I, *Pieris brassicae* Linnaeus; J, *Pieris rapae* Linnaeus; K, *Pieris napi* Linnaeus; L, *Pieris melete* Ménètriës; M, *Pontia daplidice* Linnaeus; P, *Colias croceus* Geoffroy.

Fig. 6. *Lycaena phlaeas* Linnaeus (Lycaenidae), hindwings. Also see Fig. 1(d) S.

Fig. 7. Nymphalidae. (a), forewings—A, *Clossiana euphrosyne* Linnaeus ($R_4$ is included and mapped as conjoined with $R_3$ and $R_2$ as it is *in situ*); B, *Clossiana selene* Schiffermueller; C, *Argynnis paphia* Linnaeus; D, *Fabriciana adippe* Schiffermueller; E, *Mesoacidalia aglaja* Linnaeus; F, *Inachis io* Linnaeus; G, *Aglais urticae* Linnaeus; H, *Polygonia c-album* Linnaeus.

(b), hindwings—I, *Vanessa cardui* Linnaeus; J, *Vanessa indica* Herbst; K, *Vanessa atalanta* Linnaeus; L, *Aglais urticae* Linnaeus (also see R); M, *Precis orithya* Linnaeus; N, *Precis aenone* Linnaeus; O, *Neptis sappho* Pallas; P, *Bematistes poggei* Dewitz; Q, *Acraea eponina* Cramer; R, *Aglais urticae* Linnaeus (also see L).

Fig. 8. *Melitaea-Mellicta* (Nymphalidae), forewings. (a) A, *Melitaea cinxia* Linnaeus; B, *Mellicta varia* Meyer-Dur. (b), *Mellicta athalia* Rottemburg (continuing to Fig. 9).

Fig. 9. *Mellicta athalia* Rottemburg (Nymphalidae), forewings, continued from Fig. 8(b).

Fig. 10. *Coenonympha* (Satyridae), hindwings. (a), (b) and (c) A, *C. pamphilus* Linnaeus; (c) B, *C. tullia* Mueller.

Fig. 11. Satyridae and Danaidae. (a) and (b), forewings—A, *Coenonympha pamphilus* Linnaeus; B, *Maniola jurtina* Linnaeus; C, *Danaus chrysippus* Linnaeus.

(c), hindwings—D, *Maniola jurtina* Linnaeus; E, *Hyponephele lycaon* Rottemburg; F, *Pyronia tithonus* Linnaeus; G, *Erebia pandrose* Borkhausen; H, *Erebia aethiops* Esper.

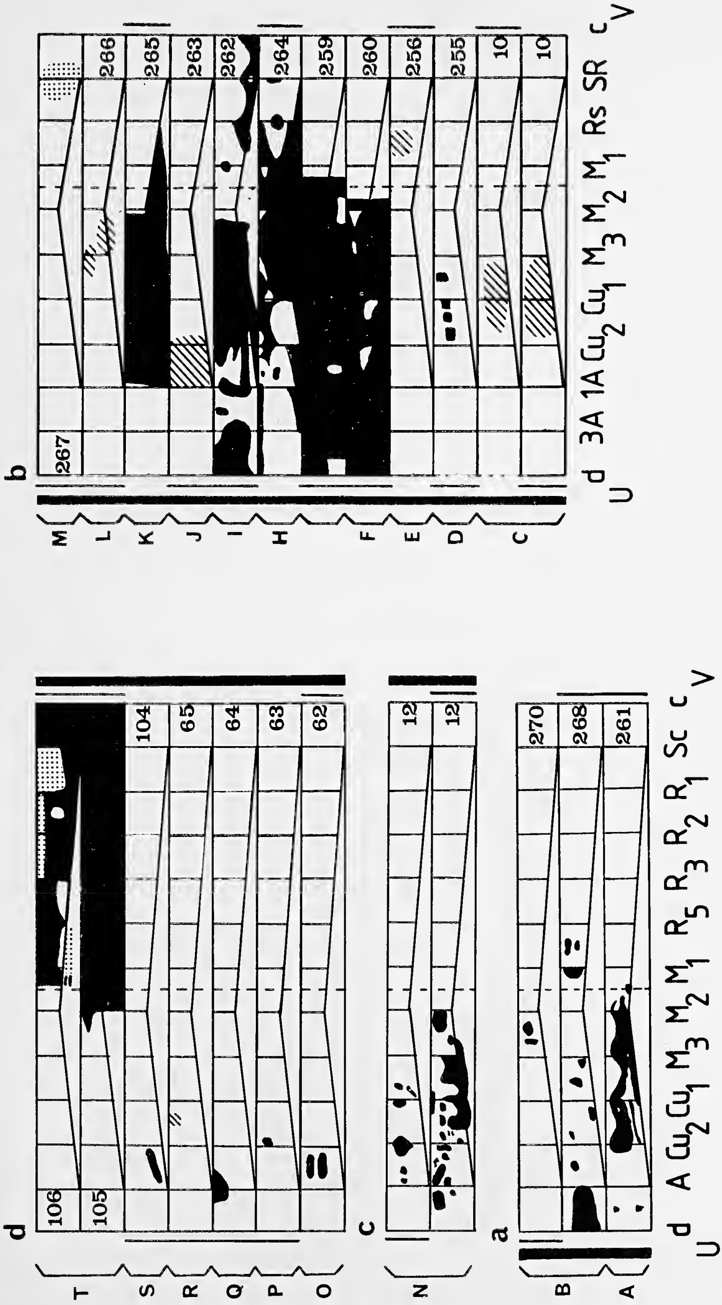
Fig. 12. D/V homoeotic mosaics. (a), forewings—A, *Colias croceus* Geoffroy; B, *Callophrys rubi* Linnaeus; C, *Lycaena phlaeas* Linnaeus; D,

*Plebejus argus* Linnaeus; E, *Polyommatus icarus* Rottemburg; F, *Lysandra coridon* Poda; G, *Lysandra bellargus* Rottemburg.
(b), hindwings—H, *Hepialus humuli* Linnaeus; I, *Pieris napi* Linnaeus; J, *Plebejus argus* Linnaeus; K, *Polyommatus icarus* Rottemburg; L, *Lysandra coridon* Poda; M, *Vanessa cardui* Linnaeus; N, *Batesia hypochloros hemichrysa* Godman & Salvin; O, *Morpho terrestris* Butler; P, *Morpho menelaus* Linnaeus.

Fig. 13. Distribution of mosaic areas and boundaries on the homoeotic wings of Lepidoptera. A revised version of Figs. 4c-f of Sibatani (1980) now based on the expanded data. The horizontal axes are divided as in Figs. 1-12, but superimposed with D which represents the discal cell, of which the rostral and caudal halves were scored and shown separately on both sides of the vertical line of $M_2$ which serves as the dividing midline of the discal cell given in broken lines. The empty and solid portions of each column represent mosaic boundaries encompassing only a part of the length of a space, and those running over 90% or more of it, respectively. The cross-hatched portion of each column signifies the 'solid' space covered over its (not necessarily proximal) 90% or more by the homoeotic element and thus virtually devoid of mosaic boundaries. (a), (b), F/H homoeosis; (c), (d), D/V homoeosis; (a), (c), forewings; (b), (d), hindwings. Total number of wing surfaces examined: (a) 173, (b) 158, (c) 13, and (d) 20.

Figs. 14-17. Color Plate, see page 46 for figure explanations.

Fig. 18. A partial duplication of the pattern on the ventral surface of right hindwing of *Plebejus argus* Linnaeus A1 ♂ from England in the L. Christie collection.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256
255
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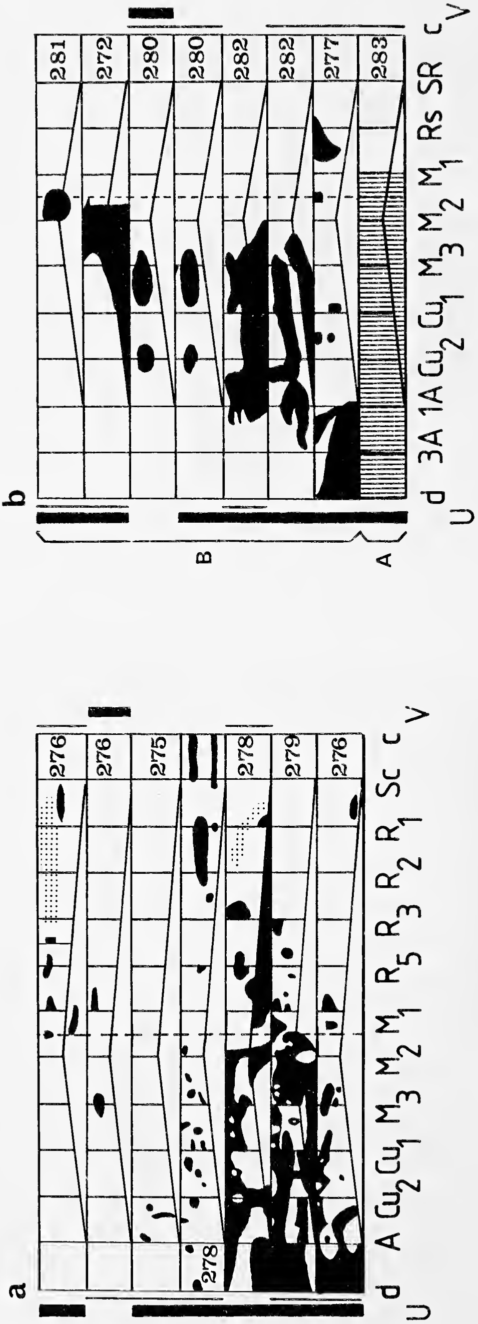
10
M
L
K
J
I
H
F
E
D
C
U d 3A 1A Cu2 Cu1 M3 M2 M1 Rs SR c V
d
106
105
104
65
64
63
62
T
S
R
Q
P
O
c
12
12
N
a
270
268
261
B
A
U d A Cu2 Cu1 M3 M2 M1 R5 R3 R2 R1 Sc c V

Figure 1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282
282
277
283
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1A
$Cu_2$
$Cu_1$
$M_3$
$M_2$
$M_1$
Rs
SR
c
U
V
B
A
a
276
276
275
278
278
279
276
d
A
$Cu_2$
$Cu_1$
$M_3$
$M_2$
$M_1$
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$R_3$
$R_2$
$R_1$
Sc
c
U
V

**Figure 2**

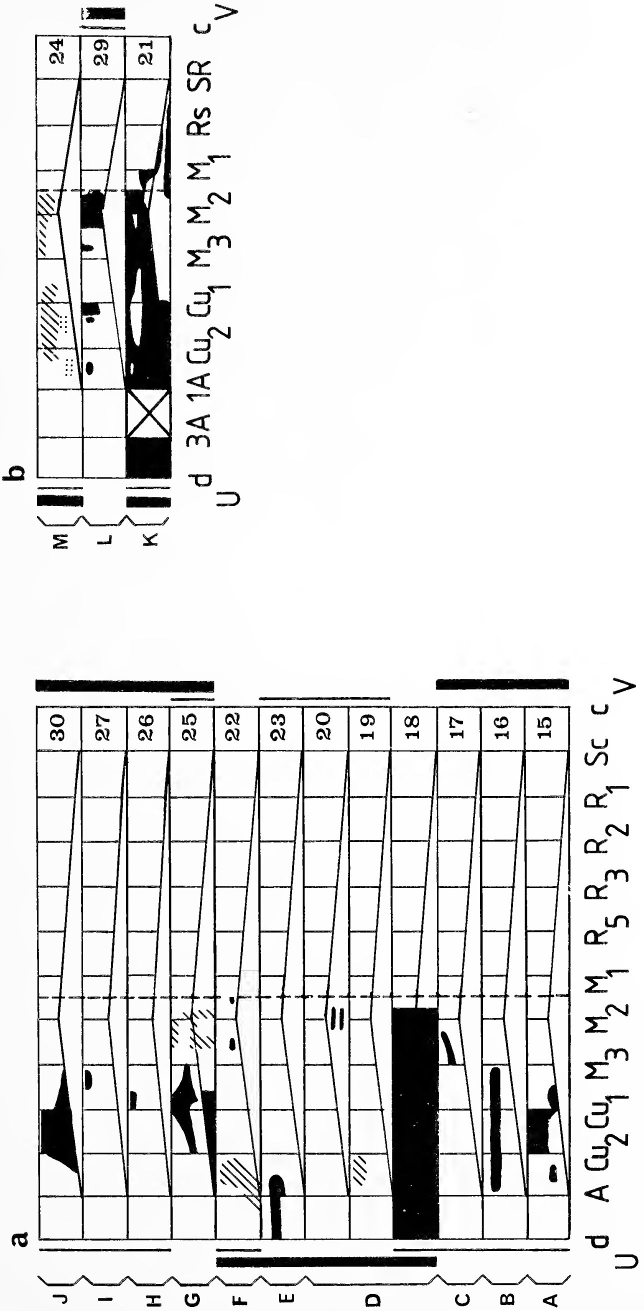
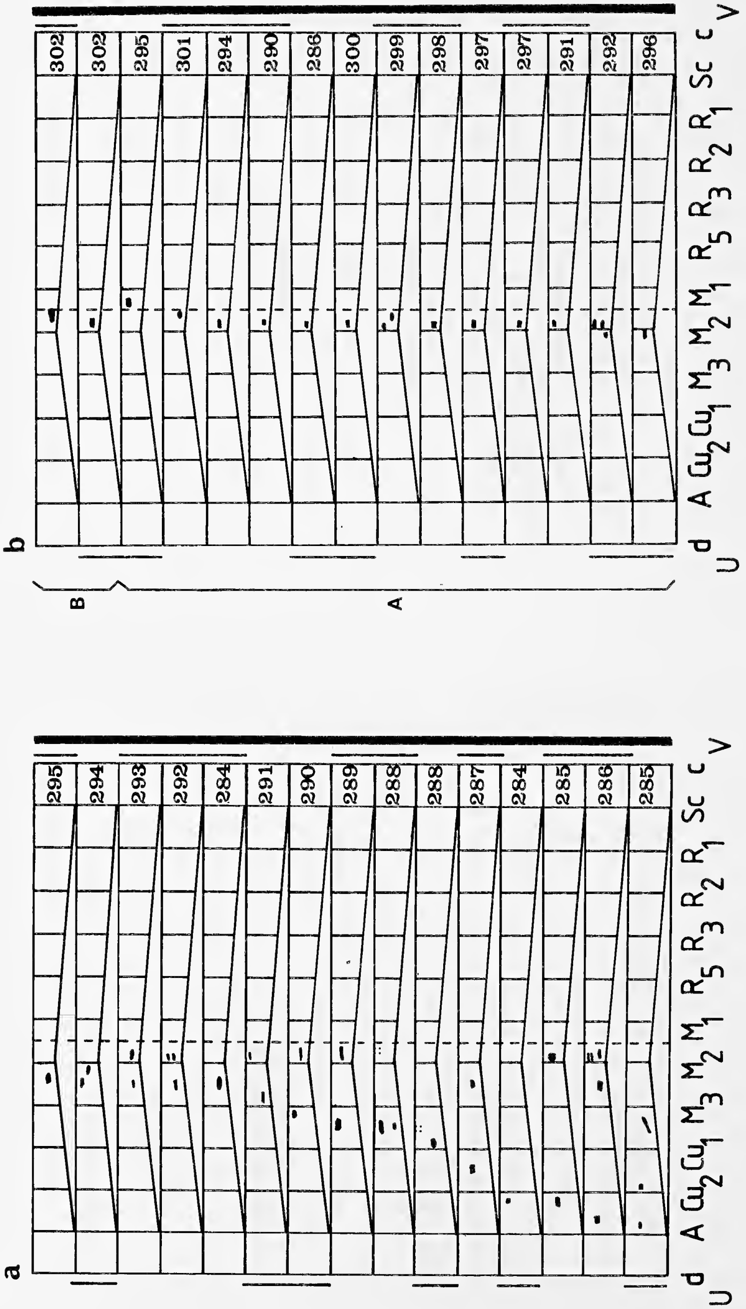

a
b
A
B
C
D
E
F
G
H
I
J
K
L
M
15
16
17
18
19
20
23
22
25
26
27
30
21
29
24
U
d
A
Cu2
Cu1
M3
M2
M1
R5
R3
R2
R1
Sc
c
V
3A
1A
Rs
SR

Figure 3


b
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301
294
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286
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297
297
291
292
296
B
A
a
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294
293
292
284
291
290
289
288
288
287
284
285
286
285
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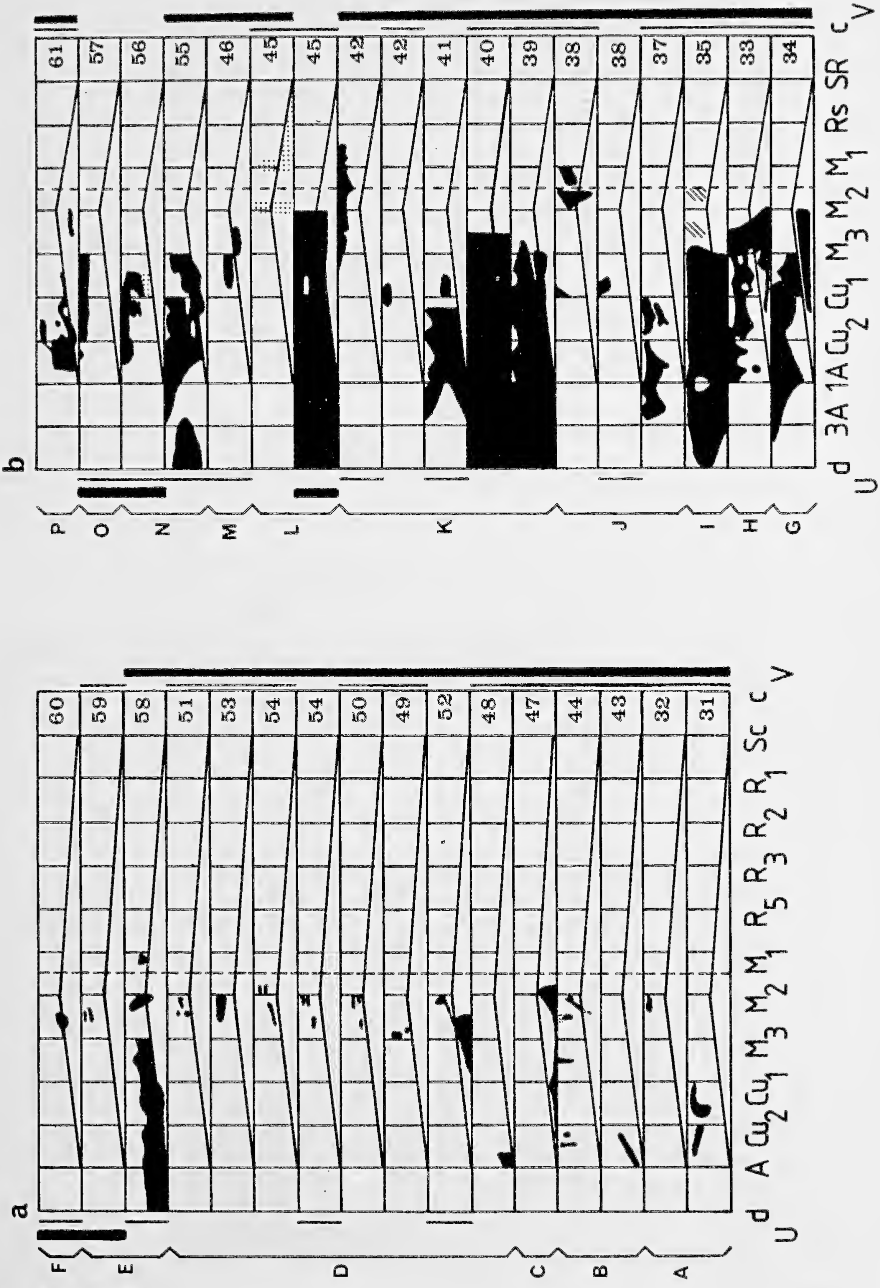
U d A Cu2 Cu1 M3 M2 M1 R5 R3 R2 R1 Sc c V

**Figure 4**


b
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61 57 56 55 46 45 45 42 42 41 40 39 38 38 37 35 33 34
P O N M L K J I H G
a
U d A Cu2 Cu1 M3 M2 M1 R5 R3 R2 R1 Sc c V
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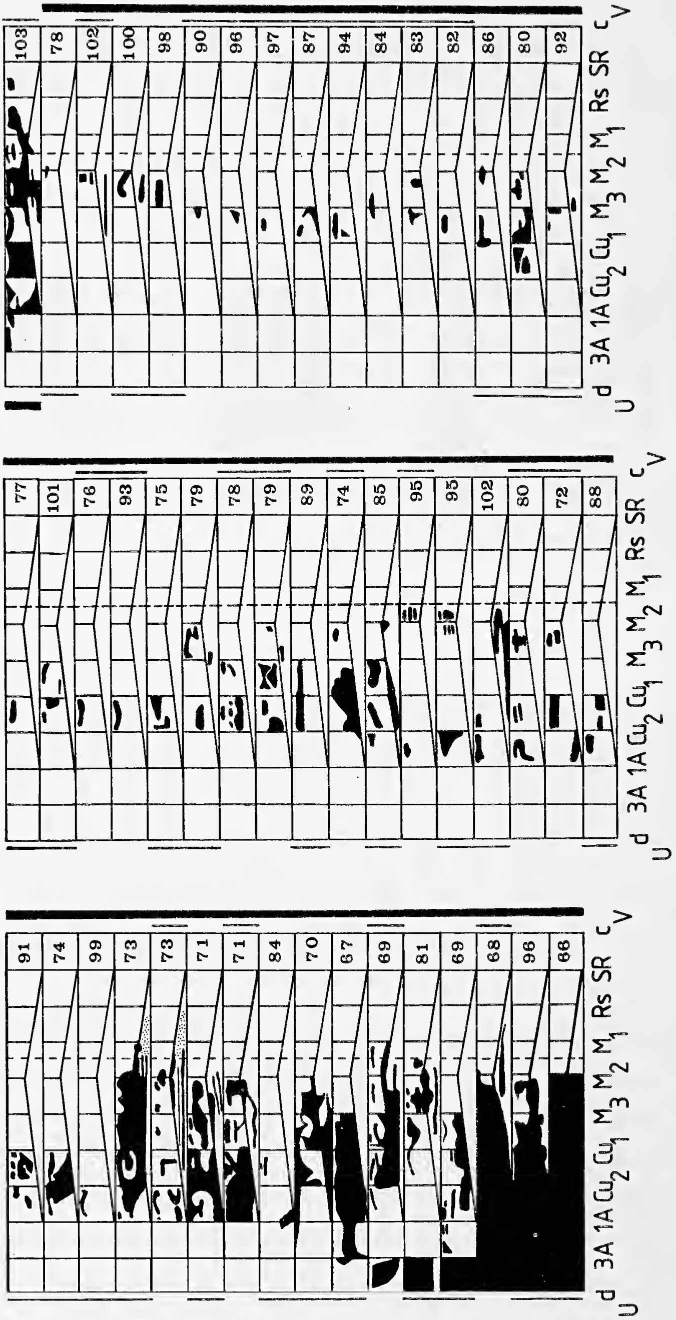
F E D C B A

**Figure 5**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102
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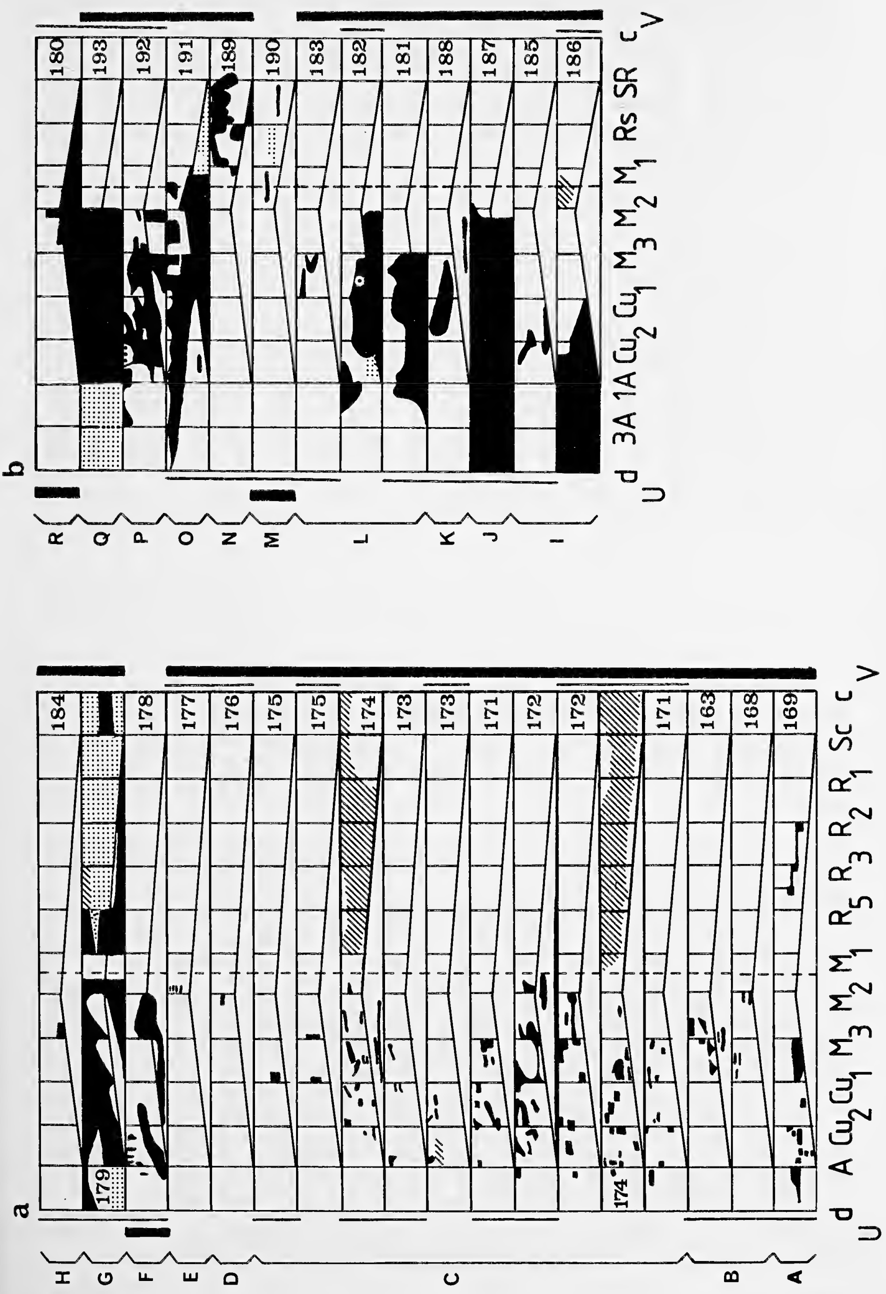
72
88
91
74
99
73
73
71
71
84
70
67
69
81
69
68
98
68
c
V
SR
Rs
$M_1$
$M_2$
$M_3$
$Cu_1$
$Cu_2$
1A
3A
d
U

**Figure 6**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F
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D
C
B
A
R
Q
P
O
N
M
L
K
J
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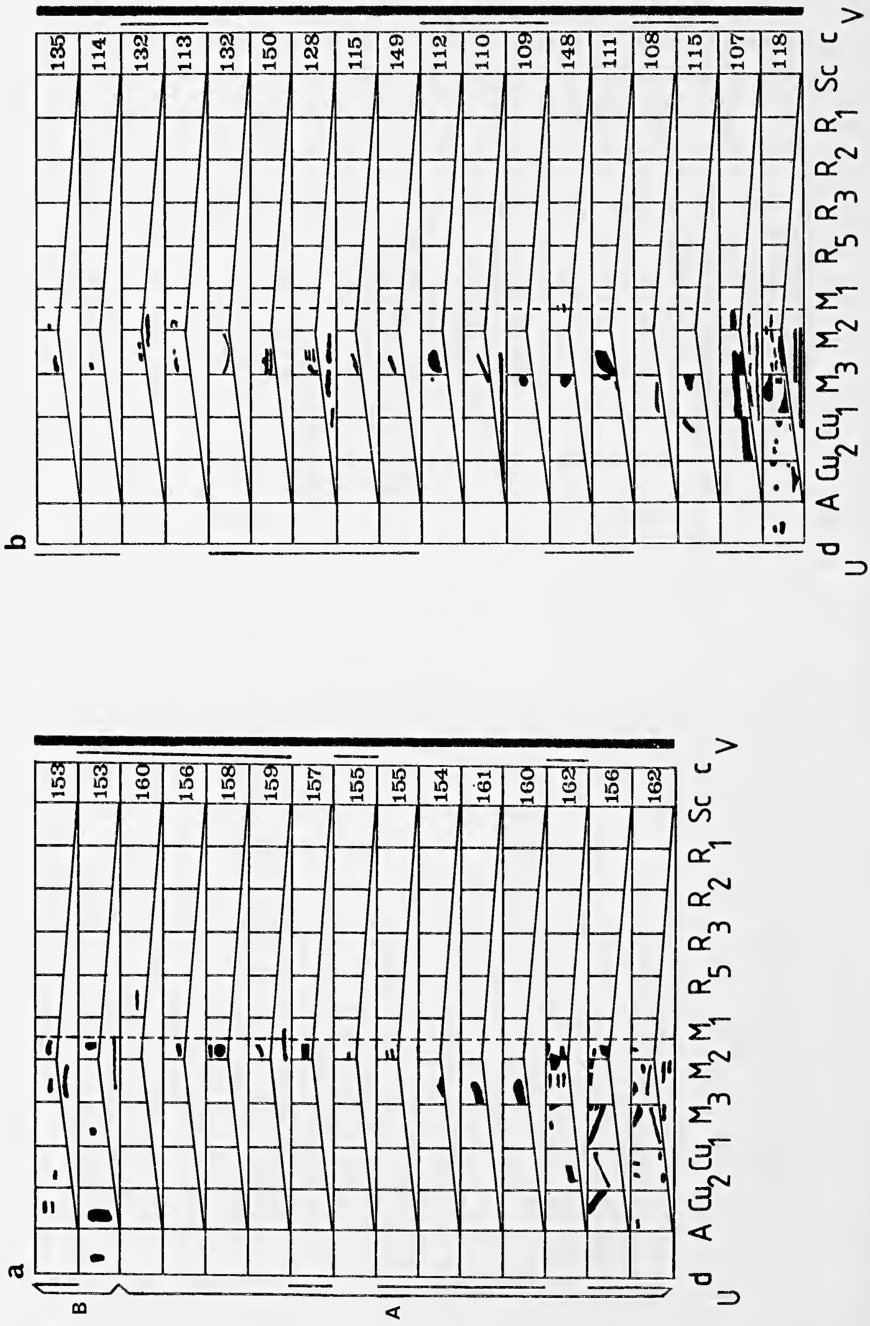
179
178
177
176
175
175
174
173
173
171
172
172
174
171
163
168
169
180
193
192
191
189
190
183
182
181
188
187
185
186
U
d
A
Cu2
Cu1
M3
M2
M1
R5
R3
R2
R1
Sc
C
V
3A
1A
Rs
SR

Figure 7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109
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111
108
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107
118
V
c
Sc
$R_1$
$R_2$
$R_3$
$R_5$
$M_1$
$M_2$
$M_3$
$Cu_1$
$Cu_2$
A
d
U
a
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153
160
156
158
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157
155
155
154
161
160
162
156
162
V
c
Sc
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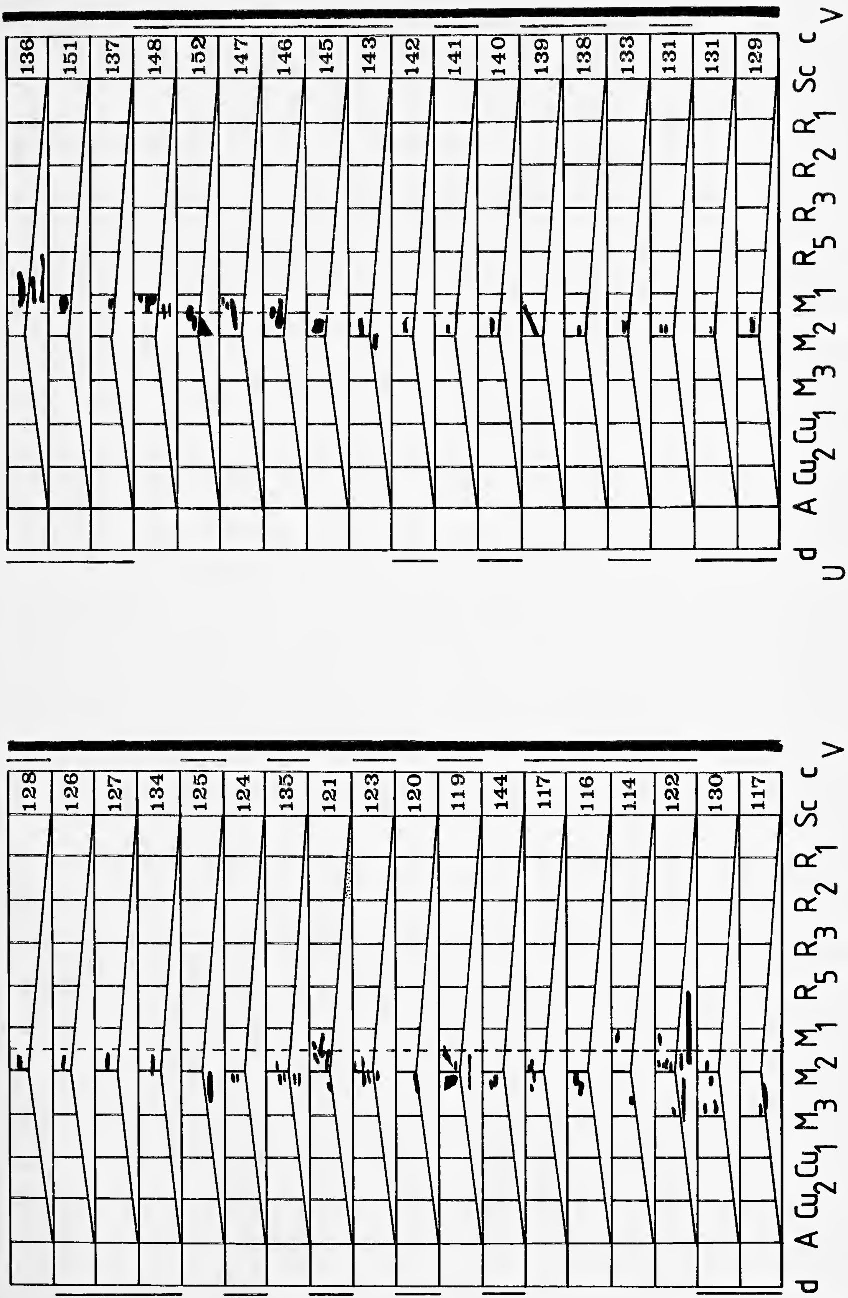
B
A

**Figure 8**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$R_5$
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$M_2$
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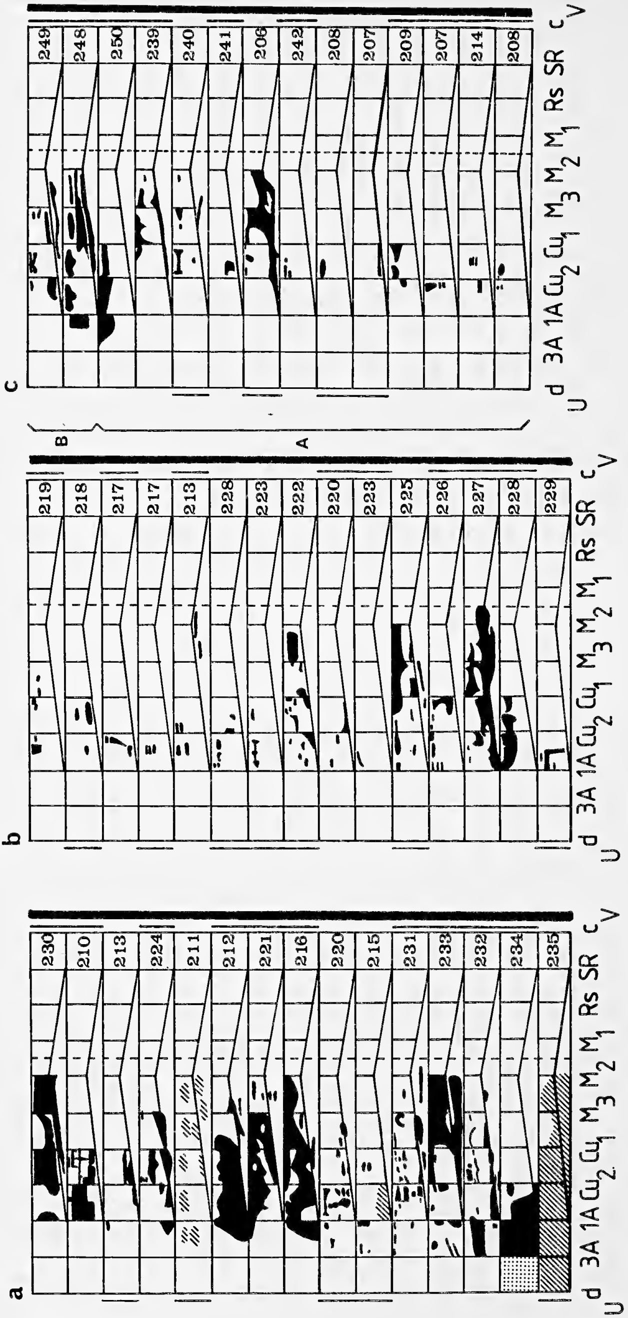
A
d
U

**Figure 9**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c
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B
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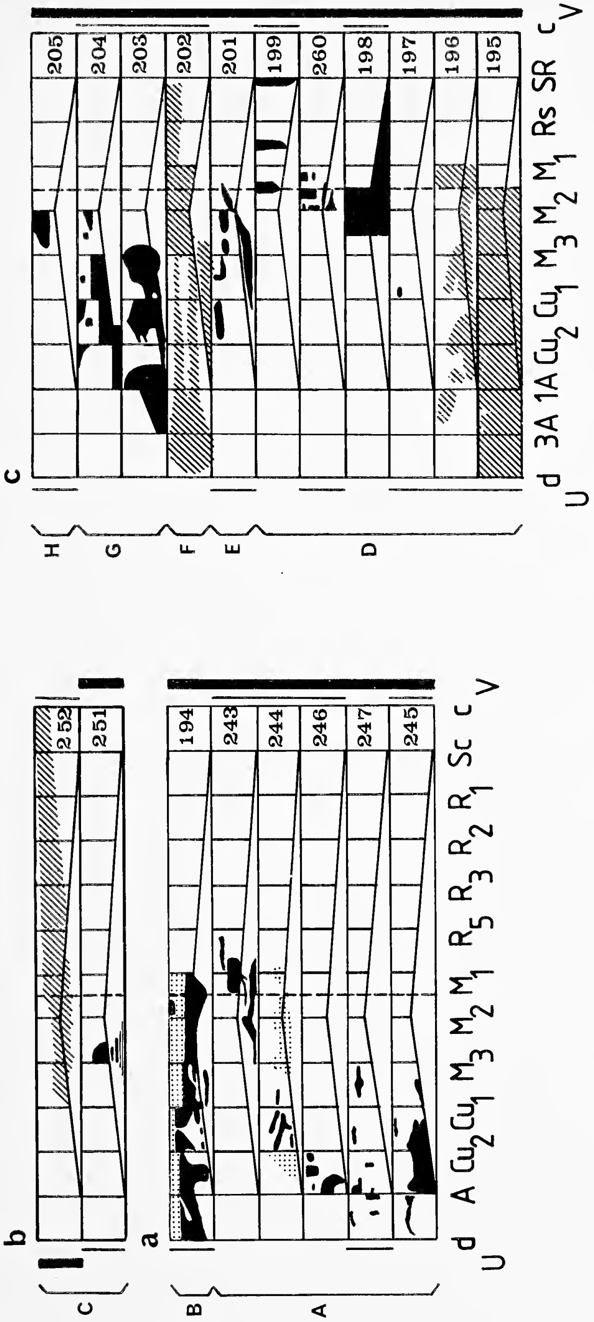
**Figure 10**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H
G
F
E
D
V c SR Rs M1 M2 M3 Cu1 Cu2 1A 3A d U
b
252
251
C
a
194
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246
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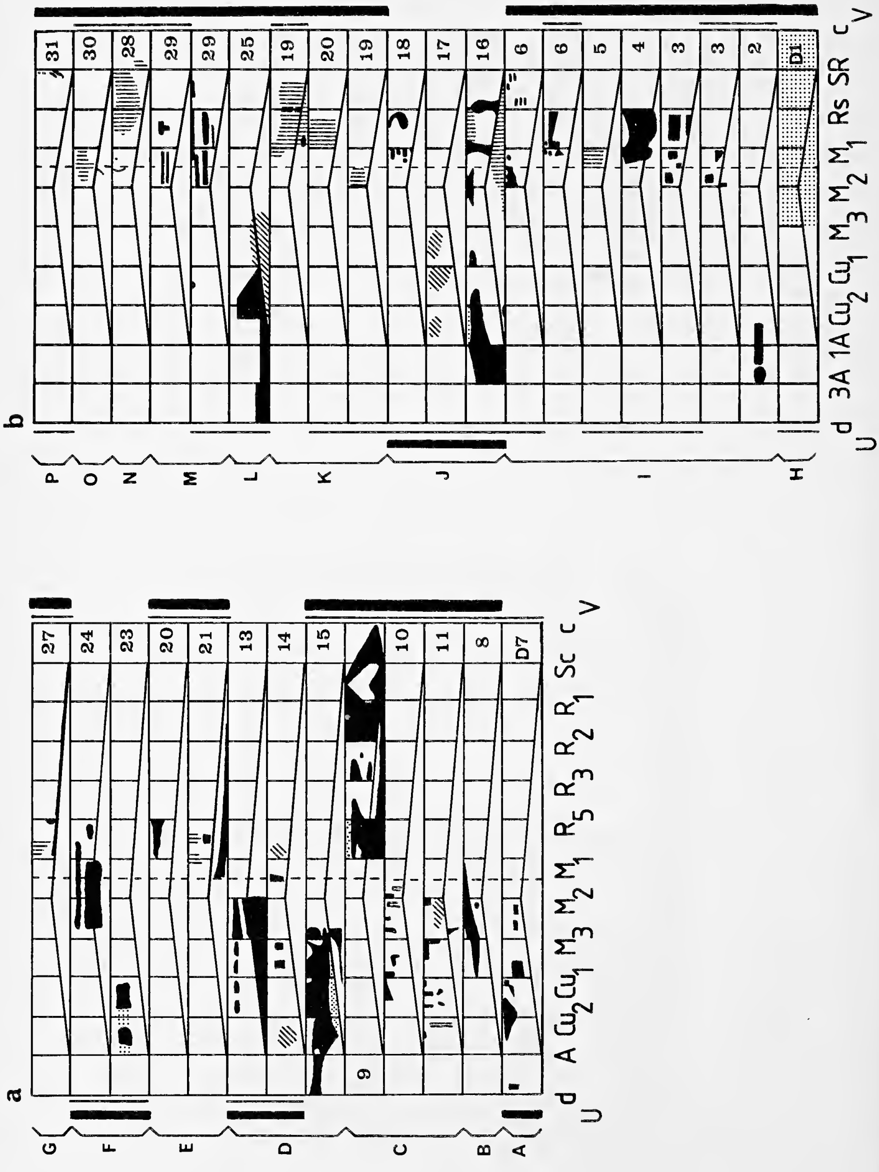
245
B
A
V c Sc R1 R2 R3 R5 M1 M2 M3 Cu1 Cu2 A d U

**Figure 11**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16
6
6
5
4
3
3
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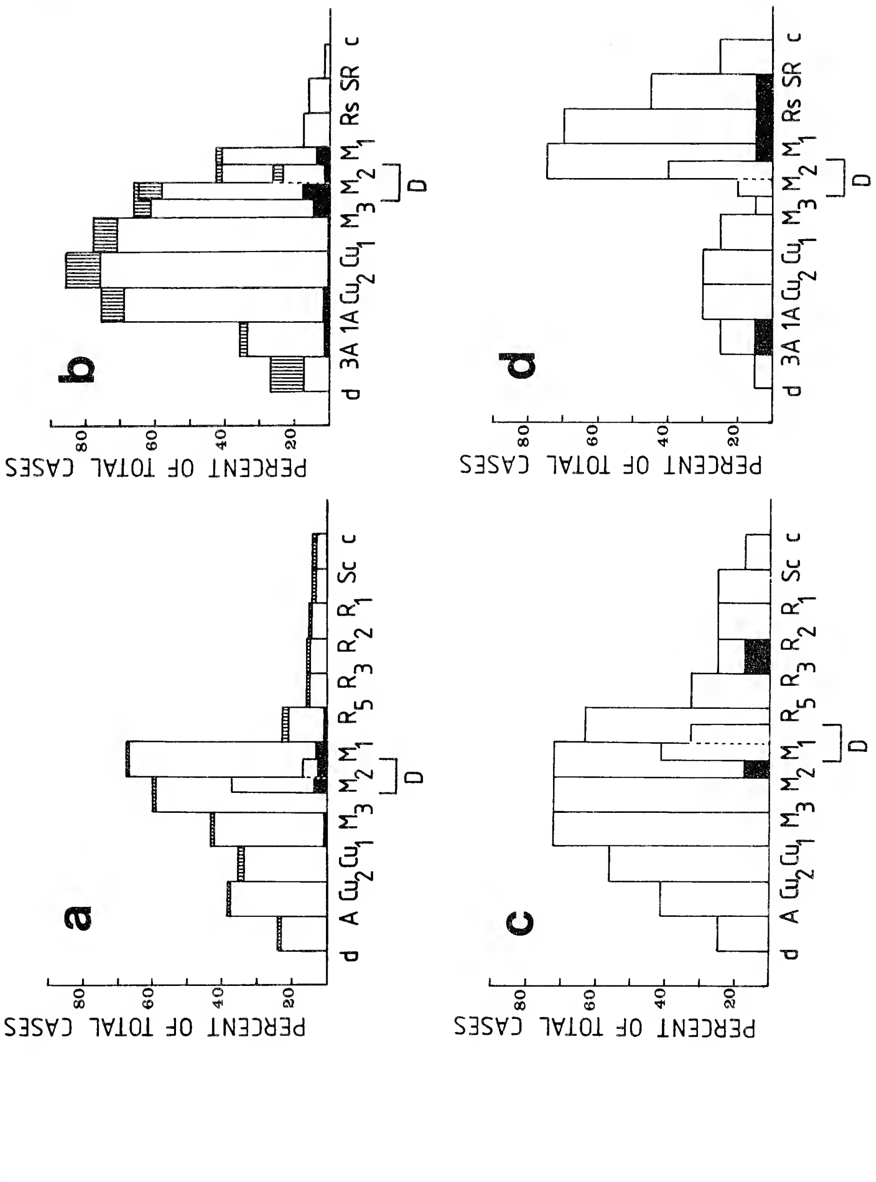
D1
U d 3A 1A Cu2 Cu1 M3 M2 M1 Rs SR c V
P
O
N
M
L
K
J
I
H
a
27
24
23
20
21
13
14
15
9
10
11
8
D7
U d A Cu2 Cu1 M3 M2 M1 R5 R3 R2 R1 Sc c V
G
F
E
D
C
B
A

**Figure 12**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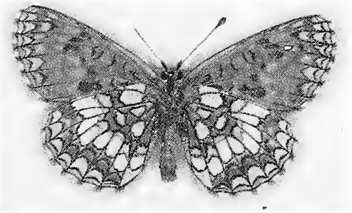
PERCENT OF TOTAL CASES
80
60
40
20
d A $Cu_2$ $Cu_1$ $M_3$ $M_2$ $M_1$ $R_5$ $R_3$ $R_2$ $R_1$ Sc c
D
b
PERCENT OF TOTAL CASES
80
60
40
20
d 3A 1A $Cu_2$ $Cu_1$ $M_3$ $M_2$ $M_1$ Rs SR c
D
c
PERCENT OF TOTAL CASES
80
60
40
20
d A $Cu_2$ $Cu_1$ $M_3$ $M_2$ $M_1$ $R_5$ $R_3$ $R_2$ $R_1$ Sc c
D
d
PERCENT OF TOTAL CASES
80
60
40
20
d 3A 1A $Cu_2$ $Cu_1$ $M_3$ $M_2$ $M_1$ Rs SR c
D

**Figure 13**



Figs. 14-17. Some examples of wing homeosis from England; all from the L. Christie collection. They will be further analysed elsewhere using black and white prints. For data, see the accompanying compilation list using the identification numbers. All the photographs including Fig. 18 were made available to me through the courtesy of R. I. Vane-Wright of the British Museum (Natural History).

Fig. 14. B130 *Mellicta athalia* Rottemburg ♂ ventral surface. F/H homoeosis on right forewing (X 1.19). See also Fig. 9.

Fig. 15, 16. *Lycaena phlaeas* Linnaeus D11 (15) and D9 (16) ♀♀ ventral surface. D/V homoeosis on right forewings (15 = X 1.36; 16 = X 1.27). See also Fig. 12(b).

Fig. 17. *Plebejus argus* Linnaeus D18 ♀ dorsal surface. D/V homoeosis on right hindwing (X 1.50). See also Fig. 12(b).

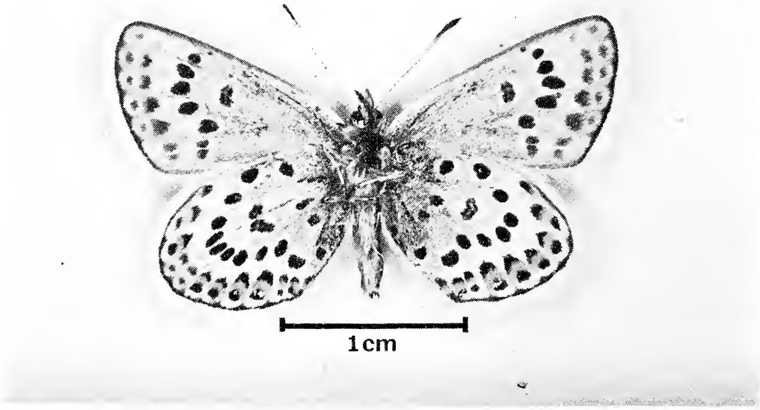


**Figure 18**

*The Journal of Research on the Lepidoptera* 22(1): 47-100, 1983

# Life History and Morphology of the Immature Stages of the Bog Copper butterfly *Lycaena epixanthe* (Bsd. & Le C.) (Lepidoptera: Lycaenidae)

David M. Wright

100 Medical Campus Drive, Lansdale, Pennsylvania 19446

**Abstract.** The first complete life history of *Lycaena epixanthe* (Bsd. & Le C.) is presented along with an ultrastructural examination of immature stages using scanning electron microscopy. The butterfly is strictly endemic to cranberry bog habitats and closely alligned with the biology of its foodplant *Vaccinium macrocarpon* Ait. Reproductive biology of adult butterflies is linked to the hostplant flowering period and the microanatomy of ova, larvae, and pupae show fine adjustments for survival in the bog. Despite its unique features, *epixanthe* is an integral part of the lycaenine group. Basic characteristics of immature and adult butterflies show close behavioral and developmental similarities with other *Lycaena.*

## Introduction

The cranberry-feeding *Lycaena epixanthe* (Bsd. & Le C., [1835]) is a diminuitive Nearctic lycaenid generally considered endemic to bog habitats. The current known range of *L. epixanthe* corresponds closely with the extent of recent Pleistocene glaciation in the eastern half of North America and includes a few refugia south of the glacial terminus on the coastal plain and in the Appalachian mountains (Wright, 1982b). Continental glacial action at its peak displaced northern biota far to the south and during is retreat left behind many poorly-drained depressions and kettles which became the boggy peatlands that harbor today's unique bog flora. Many acid-loving ericaceous plants flourish in these bogs, including large cranberry *Vaccinium macrocarpon* Ait. and small cranberry *V. oxycoccos* L. The butterfly is tied strictly to bog habitats where cranberry can grow and its biology is totally adapted to its relationship with this plant. On the whole, the life history of *L. epixanthe* is still quite fragmentary and nearly all present-day lepidopterological literature describes the immature stages as largely unknown. The intent of this study is to present details of *epixanthe*'s life history and to describe the microanatomy and chaetotaxy of the immatures using scanning electron microscopy.

## Historical Synopsis of Previous Works

Brief aspects of historical studies on the life history of *L. epixanthe* have been summarized previously by Wright (1982a). The search for the foodplant and immature stages brought repeated failures to many who had sought them. In some of his very first writings, Scudder (1868, 1869, 1872) noted that *epixanthe* adults were associated with cranberry and even nectared on the blossoms. Yet he persisted to believe throughout his career that the foodplant was one of the Polygonaceae, particularly swamp dock *Rumex verticillatus* L. (Scudder 1876, 1889, 1893). Guesswork by many early authors lead to several erroneous foodplant entries in Tietz's (1972) life history compendium. The foodplant was eventually discovered in 1907 by Cook and Watson (1908) who observed oviposition firsthand on *Vaccinium macrocarpon* in New Jersey. Since the discovery of the foodplant, the immature stages have received very little attention and no single work is complete. The white echinoid ova were first described by Saunders (1869) and later by Scudder (1889), both from artificially obtained ova. Scudder· (*loc. cit.*) included three illustrations of ova in his voluminous work (Pl. 65, Fig. 16 & 23; Pl. 68, Fig. 11), but his first figure was unrecognizable and contrastingly different than the latter two. This discrepancy can be attributed to the fact that Scudder commissioned several artists to render illustrations. Scudder (*loc. cit.*) also examined a "dead and dried" first instar dissected *ex ovum* from which he gathered very little detail. His attempt to picture the head capsule (Pl. 79, Fig. 41) yielded a paucity of cranial setae and an inaccurate fronto-clypeal apotome. It was not until many years later that live larvae were actually observed for the first time. Franklin (1948) in the miscellaneous section of his "Cranberry Insects in Massachusetts" published a photograph of an *epixanthe* mature larva and pupa. The photograph was not accompanied by descriptive text and stood alone with legends only. Despite its shortcomings, Franklin's photograph was the first of its kind and it went virtually unnoticed by the lepidopterist community. Plath (1978) was the first to successfully undertake a rearing study of *epixanthe*. Unfortunately, his sketchy paper described only a brief three-instar larval development in which the "date of hatching was not known." It is now confidently known that *epixanthe* has a four-instar larval development and Plath's instars were mislabeled after the crucial first instar was missed.

## Materials and Methods

The study site was Forge Pond bog in the New Jersey pine barrens where an *epixanthe* colony was discovered in 1976 and has been under continuous investigation since. Forge Pond lies adjacent to Nescochague Creek in the southwest corner of the Wharton State Forest (Atlantic Co.) and can be located on the USGS Atsion Quadrangle (7.5 min. series) at 39 38′55″ N latitude, 74 40′05″ W longitude. The bog is an abandoned meander of the nearby stream and is best characterized as an oxbow bog. Water depth is generally very shallow and maintained by seepage from the high water table of the underlying sandy soils. To a certain extent, stream overflow following heavy rains also contributes to the water level. The flora is very typical of New Jersey pine barren bogs where marsh-like vegetation is dominated by open wet stands of sedges and sphagnum ground cover. Chief sedges at Forge Pond are coastal sedge *Carex exilis* Dewey, twig rush *Cladium mariscoides* (Muhl.), and white beaked-rush *Rhynchospora alba* (L.). The sphagnum bog flora is very acidic and supports a luxurious growth of cranberry *Vaccinium macrocarpon* Ait. which grows as a low trailing vine running over the surface of the bog between sedge blades. Dwarfed cedar trees *Chamaecyparis thyoides* (L.) appear occasionally in the center of the bog, but generally they form thick stands of taller trees around the bog perimeter. A diverse association of herbaceous bog flora, including carnivorous plants and orchids, blooms in the wetter areas of the bog throughout the warmer months. Further details of the Forge Pond flora may be found in Thomas (1967).

In 1981, the *epixanthe* colony was observed throughout its entire flight period (12 June to 10 July) with careful attention paid to the biology of adult butterflies (e.g. basking, nectaring, courtship, pairing, oviposition). Where possible, interesting facets of adult life were recorded on 35 mm film for re-examination at later dates. A few freshly oviposited ova (three) were marked in the bog for identification in the following spring of 1982. A second larger batch of ova (198) was obtained for rearing studies by artificially confining seven gravid females (captured 22-24 June) with their foodplant in a wooden rainbarrel. The rainbarrel measured one meter in height and one meter in width, and contained an intact segment of the bog surface removed *en bloc* from the natural bog. Wire screening covered the opening at the top of the barrel. After confined females had expired, the total number of ova was counted and an average index of fecundity (ova/female) calculated. Diapausing ova remained outdoors throughout the study to assure that ambient temperatures and weather conditions were as close as possible to the natural state. Water was added periodically to the barrel to maintain moisture in the sphagnum covering and cranberry leaves. In a separate experiment, six cranberry shoots with their ova were clipped and removed from the rainbarrel and maintained in open glass jars without water. This was done in order to determine the effect of lack of moisture on ova viability.

Once hatching began in the spring of 1982, larval development was followed carefully in the natural bog and under experimental conditions. To ensure proper collection of individual larval data in the rearing experiment, tiny first instars were removed from the rainbarrel and transferred to individual potted plants. These plants were propagated from natural cranberry and rooted in soil consisting of half sand and half peat. They required regular watering and fertilizing (Osmocote). Developing larvae and pupae were examined several times daily and photographed to permanently record their growth, coloration, and behavior. Approximately six representative specimens of each larval instar and the same number of pupae and ova were submitted for scanning electron microscopy (SEM). A few exuviae of fourth instars were similarly examined.

SEM of ova, larvae, and pupae was performed with a Philips SEM 500 (Eindhoven, Holland) using an accelerating voltage of 25 kV and tilt angle of zero degrees. For studies of ova, individual cranberry leaves with an ovum attached were mounted directly onto SEM stubs using double-sided tape and then coated with 360 A° of gold-palladium (40/60) in a Polaron E-5000 sputter coater (Hertfordshire, England). Larval exuviae were mounted and coated in the same fashion. All live larvae and pupae were first fixed and then critical-point dried prior to coating. This was done to prevent shrinkage of soft tissues and to help ensure accurate morphological determinations. Larvae and pupae were fixed in 3% buffered glutaraldehyde (pH 7.2 with 0.1M sodium cacodylate buffer) for two hours at room temperature (22-25°C). Occasionally, some of the larger specimens (fourth instars) were fixed overnight in the refrigerator (4°C). Refrigerated samples were allowed to warm to room temperature prior to dehydration. All fixed samples were dehydrated in a graded series of acetone (30-100%) with approximately five minutes in each acetone strength before transfer. Following dehydration, they were promptly placed in a liquid CO2 chamber and critical-pointed dried after the acetone had been flushed from the tissue. They were then promptly mounted onto SEM stubs with double-sided tape or conductive paint for larger specimens and sputter-coated with 360A° gold-palladium (40/60). Earlier instars were mounted still attached to cranberry leaves which acted as a convenient vehicle for transfer. Most specimens were examined immediately in the SEM. Some were held in dessicant jars containing granular phosphorus pentoxide (Granusic). Under such conditions, they could be stored for long periods of time without deterioration. All SEM photographs were taken with Polaroid 55 positive-negative film.

Ultraviolet photography (UV) was used to study pinned adult specimens following the method of Ferris (1972, 1975). A 35 mm single lens reflex camera with Wratten 18A filter (Kodak) recorded images of UV reflectance on 400 ASA film (Tri-X). The specimens were illuminated by two 15-watt blacklight blue bulbs (Westinghouse) at a distance of six inches.

All setal maps of larval cranium, body, and prothoracic shield were reconstructed from SEM micrographs. In describing the chaetotaxy, the terminology and conventions of Hinton (1946) were heavily relied upon. Hinton's work is the nomenclatorial system familiar to most larval workers. With a few minor modifications for the cranium (Hinton, 1947) and prothoracic shield (Hinton, 1956), Hinton's system is still very suitable for current larval studies. Downey has adapted the Hinton system for use with lycaenid larvae (Lawrence and Downey, 1966; Downey and Allyn, 1979) and the present study used the Hinton system in much the same fashion. Parenthetically, it should be stated that usage of this system was for the convenience of naming setae only. Setal origins and homologies were not implied. Terminology of ova morphology conformed to that used by Downey and Allyn (1981) in their survey of lycaenid ova. Terminology of pupal stridulatory and associated structures followed that of Downey (1966) and Downey and Allyn (1973). All generic names of butterflies were from Howe (1975) where Nearctic lycaenines were placed in the single genus *Lycaena*. Generic names of Scudder (1876) and Miller and Brown (1979, 1981) were regarded as subgenera. Plant names followed 8th edition Gray's Manual of Botany (Fernald, 1950). For proper spellings and dates of Boisduval and Le Conte's *Hist. Lepid. Amerique sept.*, the in-depth study of Cowan (1969) was consulted.

## RESULTS

### *Biology of Adults*

In six continuous years of study (1976-1981), emergence of adult butterflies was uniquely timed to occur with the beginning of the cranberry flowering period. Furthermore, the full duration of the hostplant flowering period and butterfly flight period closely paralleled one another from year to year. The flight period averaged about four weeks. Males appeared first and were followed several days thereafter by females. Peak numbers of males and females appeared in the second and third weeks. Towards the end of the flight period, females predominated, and usually during the last week of the flight period only worn females could be seen. In 1981, the first males appeared on 12 June and the last female was seen on 10 July.

Individual butterflies were invariably associated with cranberry plants all day long and seldom were seen far from the hostplant. They nectared almost exclusively on cranberry blossoms throughout the day (0900-1900 hrs.) and only on two occasions was another nectar plant observed being used. Both observations occurred early in the flight period when two males briefly visited goldcrest *Lophiola americana* (Pursh) growing in the center of the bog. In addition to nectaring, many adults were also seen imbibing drops of water trapped on sedge stems and the sphagnum surface. This behavior seemed deliberate especially on very hot days, when they probed the vegetation surface with their proboscis presumably in search of moisture. During cranberry flowering, the diversity of bog butterfly fauna was limited and interspecific competition for nectar resources was minimal. In addition to *epixanthe*, the sedge-feeding hesperiids *Euphyes dion* (W. H. Edwards) and *E. bimacula* (Grote and Robinson) were present in small numbers; and the marsh grass satyrid *Euptychia areolatus septentrionalis* (Davis), while occasionally abundant, did not nectar. Honeybees and bumblebees were the primary cranberry pollinators. On occasion, their busy activity displaced nectaring *epixanthe* adults from cranberry blossoms. Generally blossoms were so numerous that butterflies were never excluded from nectar.

Courtship and pairing always took place in the vicinity of cranberry. In search of potential mates, males perched and darted out to investigate passing objects. While cranberry was the preferred perching plant, a few males were seen perching on sedges, goldcrest, and small cedar saplings. Both males and females began early morning basking around 0800. Following this, males generally began to perch about 1000 with many of them continuing to bask simultaneously as they perched. Peak perching activity took place in the early afternoon and gradually stopped around 1800. Perching was intermittently interrupted to nectar on cranberry blossoms. After 1800, both males and females showed little interest in courtship and spent their time nectaring and basking in the setting rays of the sun. The sun tended to "set" early in the bog due to the border of tall surrounding cedar trees.

When perching males flew out to investigate a passing butterfly, a brief spiral encounter usually occurred. If the subject investigated was another male, the encounter ended quickly. If it was a female, she usually landed promptly within seconds after the beginning of the encounter flight. Following this, the courting male landed quickly behind her, initiated a flurry of rapid wing vibrations, and attempted copulation within seconds. An unreceptive female flapped her wings strongly as part of a "rejection signal" which indicated she was previously mated. Most males promptly flew away after seeing the female's flapping wings. However, if the female was receptive, she was quiescent and copulation would take place immediately (Fig. 1). Most copulations took place on cranberry vines or redroot *Lachnanthes tinctoria* (Walt.) (Fig. 1) and were observed in the early afternoon hours (1200-1400) during peak male perching activity. A rare late afternoon mating (1615) was noted on one occasion. One coupled pair was observed in flight with the larger female leading.

Coupled butterflies usually remained *in coitu* for approximately thirty minutes. Oviposition commenced two to three days after mating.

Oviposition was observed to occur mostly in the late morning to mid-afternoon (1100-1415). The technique of oviposition was characteristic. Females typically selected cranberry plants at the edge of the bog where the hostplant was densely covered and hidden by sedges, particularly *Carex exilis* Dewey and *Cladium mariscoides* (Muhl.). After first landing on the sedges, the females then walked down the sedge stems nearly disappearing from sight. When they reached the hidden cranberry vines below, they transferred to the hostplant and selected a single leaf about three to eight cm. from the tip of a fresh shoot where they deposited a single ovum on the leaf undersurface. Most of these ova came to rest about ten to twenty cm. above the sphagnum surface of the bog floor. On occasion, ovipositing females were observed to nectar on the same cranberry plant upon which they had just oviposited or were about to oviposit. Under experimental conditions, seven gravid females confined within the cranberry-containing rainbarrel oviposited 198 ova yielding an index of fecundity of approximately 28 ova/female.

Adult *epixanthe* from Forge Pond bog were polymorphic for ventral coloration, a condition observed in each year of study. Although yellow is the typical ventral color for the eastern subspecies *L. e. epixanthe*, the Forge Pond population had small numbers of both sexes which were gray to gray-white (Fig. 1). This gray morph accounted for approximately 5% of the population and did not exhibit any noticeable behavioral differences. The yellow/gray polymorphism was not confined to Forge Pond and was uniformly noted in series of *epixanthe* collected in several other bogs within the New Jersey coastal pinelands. The low-frequency gray morph was compared with the holotype and a long series of the typically gray midwestern subspecies *L. e. michiganensis* Rawson. The two were virtually indistinguishable.

Adult butterflies at Forge Pond demonstrated the expected sexual dimorphism in ultraviolet (UV) reflectance. Males showed very strong UV reflectance in the discal regions of both dorsal wing surfaces (Fig. 9). This reflectance corresponded very closely with the "visible" wing iridescence seen with the human eye in the proper angle of sunlight. The male's discal UV reflective areas were surrounded by a broad border of non-reflective black, especially on the DHW. The female was entirely non-reflective in the discal regions. Some females had a short row of inner submarginal HW lunules which reflected stongly in UV (Fig. 10). In visible light, these scales were light silver in color and scarcely perceptible. They were immediately medial to the orange marginal lunules and the series of submarginal black maculations. Maculations and veins of neither sex were reflective in UV.

## *Biology of Immatures*

Newly oviposited ova were bright pure white in color (Fig. 2), but dulled very slightly after a few days as the embryonic larva developed. This was most noticeable in the depth of the chorionic pits and micropylar region where chorionic thickness was minimal. Two ova were dissected at 10 days of age showing embryonation complete and fully-developed first instars present. These larvae were quiescent and appeared to be in diapause. None of the remaining ova hatched until the following spring. Six cranberry shoots that were clipped and removed from the rainbarrel were completely dessicated within one week's time; diapausing larvae within the ova were also dessicated and dead.

In the following spring (1982), winter-like conditions lingered into April. Snows occurred on 6 and 9 April, and cool weather kept daytime maximum temperatures at 4.4°C (40°F). A slow warming trend began on 11 April and peaked on 16 April with a high temperature of 23.3° C (74° F). First instar larvae began emerging on 16 April and continued emerging until 27 April. Emergence took place through a small exit hole chewed in the top of the ova. No further feeding on the eggshell was noted. Tiny first instars were very mobile from the start and generally moved to positions on other cranberry leaves within minutes. Resting concealed on ventral leaf surfaces (Fig.3), first instars ate holes in the undersurface parenchyma. A protrudable head and neck made it possible for the larvae to widen and deepen these holes, but the upper epidermal surface of the leaf was never broken. Leaves bearing these holes quickly became discolored and displayed small brown blotches when viewed from above. Scanning the cranberry leaves for these blotches became a very good search method to locate larvae. Usually three to four holes were made per leaf. (See leaf at bottom of Fig. 3). Larval movement was not confined to leaves of a single vine. All instars moved freely onto adjacent vines at points of contact. (Mature instars were even seen crossing 1-2 cm. of sphagnum in order to reach another vine.) Feeding, as a rule, took place during warm daylight hours and larvae rested at night. Freshly molted larvae did not consume exuviae.

Second instars, like the first, fed almost exclusively while concealed on the ventral leaf surfaces (Fig. 4). Both first and second instars have bold dorsal red stripes patterned against a green body color. This provided a large element of camouflage for the young larvae as they blended with the green leaves and red stems of the cranberry plants. A few slow-developing second instars were still present at the time when new cranberry shoots began to unfurl (mid-May). These instars were able to eat entire leaves at the tip of the supple shoot and, even though exposed in this situation, they were still nicely camouflaged.

Third and fourth instars fed entirely on new tender shoots (Figs. 5 & 6). They were now large enough to eat full-thickness leaves and fourth instars even consumed stems and an occasional embryonic flower. Third instars had a small residual dorsal red stripe, while fourth instars were solid green. Even though these larvae remained openly-exposed in their positions on the new shoots, they were extremely difficult to detect. Their green body surface had a distinct matt appearance which produced considerably less spectral reflectance than earlier instars. No larval predators or parasitoids were observed and at no time were larvae attended by ants.

Nearing time for pupation, fourth instars selected the underside of a low-lying cranberry leaf on which they spun a silk pad for cremastral hooks and an arched silk girdle for pupal support. The girdle usually came to lie in the dorsal intersegmental groove between the second and third abdominal segments. Although fourth instars at maturity (15 mm.) were somewhat longer than most cranberry leaves, the prepupal larvae (Fig. 7) contracted considerably to conform to average leaf size (9 mm.). The green-colored pupae (Fig. 8) were speckled with black spots and remarkably well-concealed beneath the cranberry leaves close to the sphagnum surface. Some pupae were actually temporarily hidden within the sphagnum when the moss expanded after heavy rains. An interesting polymorphism for pupal color was noted. Approximately 5% of the pupae were solidly dark purple in color without noticeable black speckling. Purple pupae yielded normal yellow adults. No ants were seen with the pupae and stridulatory pupal sounds were not heard in the bog.

Stridulation in experimental conditions is still under investigation.

The total period of development from larval emergence to adult eclosion ranged from 52-60 days (ave. = 54). The four-instar larval period averaged 41 days and the pupal period 13 days. Average duration of each larval instar was 11, 9, 7, and 14 days respectively. Each instar terminated with a one to two-day period of inactivity prior to molting. The rate of growth during each instar, exclusive of pre-molt quiescence, was respectively 0.12, 0.36, 0.60, and 0.58 mm./day. In accordance with Dyar's rule (Dyar, 1890), there was a regular progression of head-capsule widths during larval development: first, .250-.285 mm; second, .380-.400 mm; third, .625-.640 mm; and fourth, 1.025-1.077 mm. Eclosion took place during daylight hours (0730-1600) and began on 7 June and lasted to 26 June.

Of the original 198 ova in the rearing experiment, 19 were destroyed by pill bugs (Isopoda) in the rainbarrel, 10 were traumatically displaced and lost during handling, six were submitted for SEM, six were used in the hostplant dessication experiment, and two were dissected to examine diapausing larvae. The remaining 155 ova overwintered, but only 56 produced live larvae. Fourteen ova contained dessicated dead larvae and the remaining 85 ova were sterile, most likely from unmated females. Of the 56 live larvae, 36 larvae and pupae were sacrificed for SEM and the remaining 20 eventually produced normal adults (12 males and 8 females).

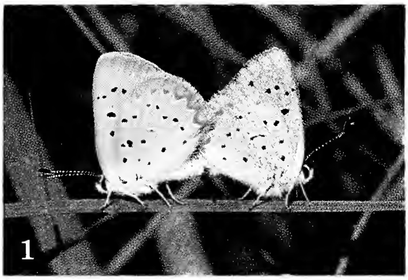
## *Morphology of Immature Stages*

### OVA

The eggs of *L. epixanthe* (Figs. 2 & 14) were upright, dome-shaped, and typical of the lycaenine type; they were round in upper view and echinoid in lateral view with the upper surface gently convex and the bottom surface flattened. The light-colored sculpturing (reticulum) of the outer chorion supplied the ova with a honeycombed or pitted appearance. The depressed pits, properly called cells, were formed within a network of intersecting chorionic ridges (muri). The ridges formed the wall-like sides of each individual cell and created small rounded prominences at points of intersection. In addition to the general configuration of the chorionic reticulum, it was not uncommon to find tiny strands of chorionic secretion (streamers) scattered irregularly over the egg surface. Measurement of six ova provided an average width of 0.75 mm and height of 0.48 mm.

The micropylar area (Fig. 18) was depressed and located in the central axis on top of the egg. It measured 0.08 mm in diameter and 0.06 mm in depth. On low power magnification, it appeared as a typical cell on the upper surface of the egg and did not influence the egg profile. The micropyle proper (Fig. 19) was a very small centrally-located, five-sided depression (pentagon) found at the bottom of the micropylar cell. Five tiny holes were located at the apices of the pentagon just beneath the lip margin. These holes varied from 0.4-0.8 microns in diameter. The pentagonal depression measured 5 microns in greatest diameter.

Figs. 1-8. Life history of *Lycaena epixanthe* (Bsd. & Le C.). Forge Pond bog, Atlantic Co., N. J. **1.** Yellow female and gray male mating, 21-VI-1981, 1.5 x. **2.** Ovum on undersurface of cranberry leaf. 13 x. **3.** First instar, 5 x. **4.** Second instar. 4 x. **5.** Third instar, 4 x. **6.** Fourth instar, 3 x. **7.** Pre-pupa, 5 x. **8.** Pupa, 5 x.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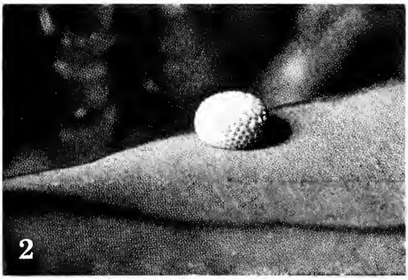
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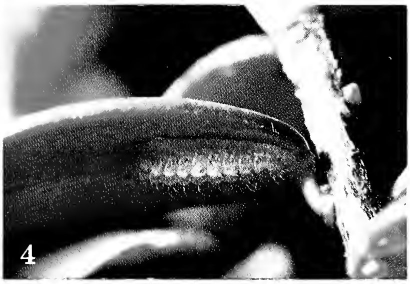
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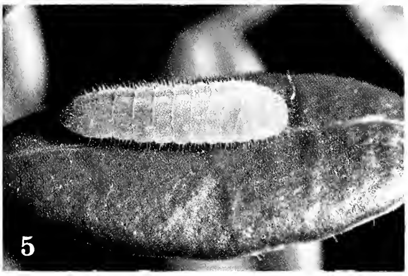
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8

Encircling the central micropyle depression was a rosette of petal-shaped cells which varied individually in size and shape (Fig. 18). Variability in rosette morphology from egg to egg was not uncommon in that some eggs had four cells to the rosette and others had five. Chorionic thickenings and bumps were frequently noted on the floor of rosette cells and incidental chorionic streamers crossing this area were also common. Occasional groups of exfoliated follicular epithelial cells were also seen. Surrounding the rosette were secondary and tertiary rows of much smaller angulate cells, completing the micropylar annulus. At the outer margin of the annulus, the walls of the micropylar region rose abruptly separating the micropylar pit from adjacent cells. There appeared to be ample air space communication between the micropylar pit and the system of air spaces beneath the sculptured chorion. Communication was accomplished via aeropyles in the annulus, open lateral recesses of annulus cells, and larger openings in the vertical side walls of the micropylar pit itself.

The system of ridges and cells covering the remainder of the egg surface followed a faint geometric pattern found in many other lycaenid ova (Figs. 14 & 15). Ridges were positioned in a series of involute curves which began at the micropylar region and coursed diagonally over the upper surface of the egg and similarly down the sides of the egg. When viewed from above, they radiated from a central axis in the fashion of a spiral nebula. Tandem pairs of curving ridges formed the opposite walls of each individual cell and, where they intersected with other ridges, formed rounded prominences. Generally, four prominences surrounded each cell and the ridge connecting each prominence had a single deep undulation. On occasion, a thin membrane of chorionic material supplied the connection in this area (Fig. 16).

The individual chorionic cells were cup-shaped and nearly circular when viewed from above (Fig. 16). They averaged 0.06 mm wide at the cell mouth and 0.02 mm wide at the base; average depth was 0.06 mm. On low magnification SEM (Fig. 15), the surfaces of the surrounding ridge tops were smooth in appearance. No aeropyles were noted on the ridges or at ridge intersections. However, at higher magnification (Fig. 6), the ridge chorion was seen to be porous containing a diffuse scattering of tiny, almost imperceptible perforations. These perforations (less than one micron in size) communicated with a network of small air spaces immediately beneath the chorionic surface (Fig. 17). Numerous perforations of larger size were located deep within the basal half of each individual chorionic cell (Fig. 16). These holes (aeropyles, plastronic pores) occurred in clusters of 20-30 per cell and averaged about 2.5 microns in diameter. They communicated with still larger airspaces beneath the chorionic surface.

The chorion in cross-section was a two-layered structure that appeared to function as an air-trapping device (Fig. 17). The inner chorion (4 microns thick) was smooth and formed a protective sphere around the oocyte and vitelline membrane. It was uniformly solid except for a small area of entrapped spongiform air cells on the dorsum of the egg surrounding the micropylar region. The inner chorion also provided support for the characteristic reticulations of the outer chorion. Intrachorionic airspaces were clearly grouped into two major subdivisions. The first and largest subdivision consisted of a series of tall chambers next to the inner chorion, partitioned by thin vertical walls of chorionic material. This subdivision occupied the lower two-thirds of the intrachorionic cross-sectional area and had direct communication with the exterior via aeropyles in the chorionic cells. The second and smaller subdivision was situated immediately beneath the highest portions of the arching ridges and contained an intricate meshwork of chorionic spokes. This subdivision communicated with the exterior via fine porosity in the surface chorion of the ridges. The two airspace subdivisions also communicated with one another by small scattered aeropyles. The entire airspace trapped between the outer and inner chorion was continous and covered the entire surface of the egg except for the flattened bottom which was appressed to the hostplant. The flat bottom contained only a smooth inner chorion.

## LARVA: FIRST INSTAR

**General.** The fully-developed first instar within the ovum measured 1.4 mm in length prior to hatching and 2.5 mm at the end of the stadium immediately prior to the first molt. Larval shape was nearly cylindrical at emergence, but assumed classical onisciform shape within the first day (Figs. 3 & 20). Body color was uniform light yellowish-green at emergence, but thereafter quickly deepened (green) and developed distinctive stripes within a few days. Stripe pattern consisted of a series of alternating red and white longitudinal lines on the major body regions (dorsal, subdorsal, lateral). (See Fig. 3). On the mid-dorsum was a bold red stripe that started on the mesothorax and continued over the abdominal segments. Prominent arching dorsal setae originated in this dorsal red stripe. (See chaetotaxy below.) At the seventh abdominal segment of several larvae, the stripe broadened and diffused over remaining segments creating a red smeared appearance. In the subdorsal region there was a series of four smaller longitudinal lines. First, a thin white line rested against the dorsal red stripe, followed in descending order by a faint broken red line, another thin white line, and a final broken red line. All of these small subdorsal lines started on the mesothorax and terminated near the seventh or eighth abdominal segment. Subdorsal and supraspiracular lenticles were incorporated into the two broken red lines. Below the subdorsal region, the lateral body area was mostly unmarked. A few larvae had an extra faint white line coursing through the abdominal spiracles, plus a row of faint subspiracular red dots (one per segment). In all larvae, the lateral ridge bore a skirt of laterally-projecting prominent setae and a bold white stripe from the mesothorax to the last abdominal segment. All chalazae were brown in color, as were the spiracles. The outer perimeter of the lenticles was brown, but the central portion was membranous and nearly concolorous with the integument.

**Integument.** The outer surface of the integument (epicuticle) had a surprisingly detailed microtopography revealed by the scanning electron microscope. In the fully expanded first instar, a large proportion of the surface integument was flat and oriented in one plane (Fig. 25). Spectral reflectance was great. Small tubercles, 2.5 microns wide and 2.0 microns high, were scattered evenly over the flat surface approximately seven to eight microns apart. Many of these tubercles terminated with a central microspine. In non-expanded first instars dissected *ex ova*, the epicuticle was contracted and wrinkled (Figs. 21 & 23). However, future tubercles could be seen at regular intervals within the wrinkled folds.

On low power magnification, a distinctive pattern of conical pits or dimples appeared in the integument on the lateral sides of each segment (Fig. 20). These pits were arranged in a regular fashion and their geometrical pattern was bilaterally symmetrical and showed no individual variation. Some pits were even present in intersegmental grooves and appeared in the same position in all subsequent instars.

Integument sculpturing may eventually prove to be useful for comparative taxonomic studies and an effort was made to describe the integument of each instar. Besides the generalized pattern of sculpturing in each instar, specialized regions of the integument (spiracles, anal folds) contained their own unique sculpturing and are described separately.

**Spiracles**. Spiracles were delimited by a sclerotized ring which surrounded a circular opening. The interior wall of each spiracle contained sculptured chitinous projections that pointed centrally into the lumen. These structures were felt to be derivatives of the integument because of their superficial location and absence from deeper endotrachea. Their pattern was simplified and consisted of 20-25 straight blunt-tipped spines (1.5-2.0 microns in length) that circled the interior spiracular wall. Pointing inwardly, they formed an effective meshwork that protected the deep-seated tracheal system.

**Cranium**. The cranium was well sclerotized and deeply black pigmented. Typical of other lycaenids, it was hypognathous-projected and capable of being deeply retracted into the prothorax (Fig. 22). Average dimensions for the first instar were width .267 mm, length .225 mm, and height .160 mm. Anteriorly, the two arms of the adfrontal sutures did not meet before reaching the cervical triangle (Fig. 11A). The frons was thus "open" and extended dorsocaudad into the cervical musculature. In live preparations, the transparent cervical musculature was observed to insert anterodorsally onto the small apical portion of the frons and dorsolaterally onto a ridge on the posterior margin of the epicranium. The clypeus was distinct and located ventral to the frons. Ocelli were present as a group of six in a circle on the lateral aspect of the head capsule. Cranial appendages will be described separately below and the reader is referred to Figures 11 and 22 for this discussion. The ventral views of Lawrence and Downey (1966, Fig. 2C) and Downey and Allyn (1979, Fig. 1) are also helpful in interpreting these complicated structures.

*Antennae*: Antennae were three-segmented and originated from a membranous area (antacoria) between the head capsule and the mandibles. They did not differ radically from other lycaenid larvae and the pattern of sensory papillae was essentially idenical. The three segments together measured 25 microns in length and the long setae of the second segment measured 80 microns.

*Labrum*: The labrum consisted of a setae-bearing rectangular plate in the midline just ventral to the fronto-clypeal region (Fig. 11 C). The inferior margin was deeply notched. Average width was 95 microns. Six setae and a puncture were present on the anterior surface. (See chaetotaxy below.)

*Mandible*: The first instar mandible (65 microns length) had five teeth (Fig. 11 D). The first four teeth (numbered anterior to posterior) were incisor-like and angled medially. The fifth and most posterior tooth was rounded terminally. This tooth was juxtaposed to the posterior mandibular condyle and two laterally-projecting setae (10 and 25 microns) which originated from the posterior lateral mandibular margin. The oral surface contained a weak ridge (retinaculum) beginning at the condyle and terminating on the opposite mandibular margin. Minor sclerotized crests ran from the retinaculum to the teeth.

*Maxilla*: The maxilla with its associated bilateral palps was very similar to that of previously described lycaenids. The free sclerotized portion of the maxillary palps contained three segments. The first segment supported a medial galea, a short forward-projecting seta (15 microns), and the remaining two palp segments. The galea and terminal palp segment contained the usual arrangement of sensory structures. The entire palp actually rested on a fourth sclerotized ring (palpifer) at its base, which in turn was attached to the membranous portion of the distal stipes (dististipes) on the ventral surface of the head. Additional setae were found on the palpifer (one, 20 microns) and sclerotized portion of the basistipes (two, 40 microns).

*Labium*: The membranous submentum resided between the two large lobes of the stipes (basistipes) and bore two ventral-projecting setae (30 microns). The sclerotized mentum was anterior to the submentum and its U-shaped arms surrounded the midline spinneret, palpiger, and paired labial palps. It then extended dorsally to parallel the hypopharynx. On the proximal portion of the mentum there were two small setae (5 microns), one on each side of the spinneret. The labial palps consisted of two segments, each with small accessory sensory structures on the tip of the second segment.

*Spinneret*: The spinneret resided midline between the maxillae on a line between the two palpifers. It consisted of a tapering tube-like distal fusulus and a proximal wedge-shaped basal component, the fusuliger. Fusulus and fusuliger measured 32 and 12 microns in length respectively.

*Hypopharynx*: The hypopharynx began as a broad flattened area anterior to the labial palps. It then continued posteriorly into the oral cavity as a smooth central trough on the floor of the mouth, flanked laterally by fleshy lobes of the paraglossae. Small tiny spines (2-3 microns) decorated the paraglossae. These spines were directed medially and often paired as doublets. No spines were observed on the hypopharynx proper.

*Epipharynx*: The membranous epipharynx lined the oral surface of the labrum and was covered with a dense layer of micropile. Three stout seta-like appendages (6 microns) were also found on the anterolateral margins of the oral-side labrum. These setae were directed in the general direction of the central labral notch.

**Chaetotaxy of Cranium.** All cranial setae of the first instar were considered to be primary setae and they persisted through subsequent instars with very little variation. They were uniformly smooth, non-spiculated, and without supporting chalazae typical of primary setae of the thorax and abdomen. Cranial setae were divided roughly into two different size groups, long and short. Long setae (tactile) were distributed evenly over the anterior parts of the head, more or less confined to those areas not normally retracted into the prothorax. Short setae (proprioceptors) were much reduced in size and number, and confined to the broad areas of the head (vertex and lateral) which easily retracted into the prothorax. Many of these setae were impossible to examine without the aid of scanning electron microscopy. Cranial punctures were also accessible to SEM study when a light coating was applied to the specimen. The reader is again referred to Figure 11 for discussion of cranial setae. Setation is described for the left half of the head capsule only; the opposite half is symmetrically identical.

*Frontal (F) and Clypeal (C) Groups*: The frons was open all the way to the cervical triangle and the apex of the frons was covered by cervical musculature. Frontal seta F1 was located at the base of the frons near its junction with the clypeus. F1 was relatively small and averaged 13 microns in length. A frontal puncture (Fa) was found medial to F1 on the same level near the midline. Clypeal setae C1 and C2 were equal in length, but considerably longer (50 microns) than F1. Along with setae of the articulated mouthparts, C1 and C2 were often the only cranial setae visible when the head was retracted deeply into the prothorax (Fig. 22). C1 was located laterally near the adfrontal suture and C2 was located medially nearer the midline. A small puncture (Ca) was found midway between C1 and C2.

*Adfrontal Group (AF)*: Closely aligned with the lateral margin of the adfrontal suture were two short setae AF1 and AF2 (8.5 microns). Both setae were located adjacent to the upper portion of the suture with AF2 dorsal to AF1. On this same line ventral to AF1 was a small puncture (AFa).

*Anterior Group (A)*: The anterior group was comprised of two setae and a puncture. A1 was immediately above the antenna close to the mandibular condyle. A2 was located directly behind it at the level of ocelli I and II, while puncture Aa was lateral to A2 in close association with the same ocelli. A2 (23 microns) was slightly longer than A1 (17 microns).

*Ocellar Group (O)*: A single short seta (01) was present inside the ocellar circlet near ocellus III. Puncture Ob, described as an accessory puncture by Hinton (1947), was situated anteriorly between ocelli III and IV.

*Subocellar Group (SO)*: Seta SO2 was the longest (50 microns) of this group and occupied a position just posterior to ocellus V. SO3 was the next longest (40 microns) and was located near the basistipes on a vertical line ventral to SO2. SO1 was the smallest member of the group (25 microns) and was found immediately beneath the antennal socket next to the mandibular articulation. No less than five punctures were found in the subocellar region. The largest puncture was located beneath SO2 and was designated SOa. Remaining accessory punctures were not named.

*Lateral (L) and Genal (G) Groups*: The lateral region of the epicranium was completely devoid of setae and punctures. Genal seta G1 was very minute (4 microns) and the only seta found on the gena. Puncture Ga was a short distance behind and above G1.

*Posterior Group (P)*: The posterior group consisted of a single seta (P1) found immediately posterior to the last member of the anterior group (A2). P1 was extremely small (4 microns) and somewhat closer to the adfrontal suture than A2. Puncture Pa was not located.

*Vertex (V) Group*: Setae of the vertex group were reduced in number and size. V1 was located lateral to AF2 and V2 was slightly posterolateral to V1. Both setae were minute (4 microns). No puncture was located.

*Labrum*: Six pairs of setae and a puncture were present on the anterior surface of the first instar labrum (Fig. 11C). Two of the setae were located on the flat facial surface (medial group) and the remainder were distributed along the inferior and lateral margins (lateral group). In the medial group, M1 occupied the innermost position with M3 just lateral to it. M3 was the longer of the two measuring 23 microns in length. The lateral group consisted of L1 and L2 on the true lateral margin of the labrum, plus L3 and L4 on the anterior margin projecting slightly medially. A small puncture was noted at the apex of the labral notch.

**Chaetotaxy of Body**. Five types of setae were found on the first instar larva. (1) Major spiculiferous setae (Fig. 13 A). These setae were generally long and measured up to 400 microns in length. They were uniformly covered with a dense cloak of distally-projecting microspines or imbrications. Each was supported by a stout smooth cylindrical chalaza. Spiculiferous setae compromised the majority of primary setae found on the body of the first instar larva. Likewise, the numerous secondary setae of subsequent instars were also spiculiferous in type. (2) Filiform setae (Fig. 13B). These setae were very fine and hairlike in appearance. The distal tip was minimally expanded and capitate. They were confined to the prothoracic shield on all instars where they probably served a sensory function. Their base was recessed into the shield in what looked like a small circular opening (puncture). Setal size ranged from very small in the first instar (40 microns) to quite long in the fourth instar (375 microns). (3) Tufted setae (Fig. 13C). These setae were moderately long (120 microns) and appeared to be modified spiculiferous setae. They were spiculated in the normal fashion proximally, but the distal third was decorated with a dense tuft of spines twice the size of proximal spiculations. Tufted setae were found only on the suranal fold of the tenth abdominal segment where they projected backwardly over the anal opening. Each was borne on a stout smooth chalaza. (4) Thorny setae (Fig. 13D). These setae were medium-sized in length (60 microns) and appeared to be a modification of smooth non-spiculated type setae. Immediately after emerging from their chalaza, they branched into multiple thornlike spines. Spines projected upwardly and outwardly from the central setal stem. Secondary branching was not noticed. These setae were located on the subanal fold of the last abdominal segment and formed part of a continuous row of subanal setae that swept under the anal opening. (5) Smooth non-spiculated setae (Fig. 13E). These setae were indistinguishable from cranial setae except for the cylindrical chalaza that supported them. Chalazae were absent on the cranium. Smooth setae varied considerably in size and accordingly were divided into two functional groups. They reached 60 microns in size in the subventral area and subanal fold where they most likely served a tactile function. On the other hand, they were truly microscopic in size (2-10 microns) on the venter and intersegmental grooves where they undoubtably functioned as proprioceptors supplying information about body movement and position. Finally, it is also probable that some medium-sized smooth setae (30 microns) functioned as proprioceptors for specialized areas of the body like the ventral prolegs.

Lenticles were also prominent features of the larval integument (Figs. 13F & 28). Their characteristic shape included a circular cone-shaped side wall which was smooth and heavily sclerotized. The pimple-like dome covering on the top of each lenticle was membranous and non-sclerotized. Perforations in the dome were not appreciated in first and second instars, but they were readily discernible in later instars. Lenticles averaged about 15 microns in height, 30 microns in width at the base, and 17 microns wide at the dome. While not derived from setal origins, they were distributed in an orderly arrangement on first instars and therefore were mapped along with setae in preparation of Figure 12. Lenticles were more or less aligned in horizontal rows in the following regions: subdorsal (SDL), supraspiracular (SSL), and subventral (SVL).

The highly-modified structures seen in Figures 13G and 13H were specialized setae confined to later stages (fourth instar and pupa). They were quite unique to *Lycaena* and apparently restricted to this group. They will be discussed separately below with their corresponding developmental stage.

In following the discussion of specific arrangement of first instar setae and lenticles, the reader is advised to refer to the setal map in Figure 12. In this figure, only structures on the left side of each segment were depicted and described. From time to time, additional reference is made to specific SEM photomicrographs to further aid the discussion.

*Prothorax and Prothoracic Shield*: The prothoracic shield was well-sclerotized and resided on the dorsum of the prothorax (Figs. 13I and 23). It consisted of two flat circular plates joined together roughly in the shape of a figure "8". A larger circular plate (130 microns) was located posteriorly and a smaller plate (60 microns) anteriorly. Four pairs of setae and a pair of lenticles were found on the shield. A major spiculiferous seta (D2) resided on the anterior margin of the anterior plate near the midline. A small apical projection of the shield separated the bases of the paired D2 setae. Just posterior and slightly lateral to D2 was a lenticle and immediately posterolateral to the lenticle was another major spiculiferous seta (SD2). This completed the complement of setae and lenticles on the anterior plate. The posterior plate had a major siculiferous seta (SD1) on its anterior margin on a line directly posterior from the lenticle of the anterior plate. SD1 was the longest seta (200 microns) of the entire shield; the other major setae were only about two-thirds as long. Posterolateral to SD1 and situated near the lateral margin of the posterior plate was a very fine filiform seta (XD2) which originated from a depressed puncture-like circular opening. XD2 averaged 40 microns in length and had a slightly clubbed distal tip.

Except for XD2, all setae of the shield attained considerable length and projected anteriorly over the head and neck in a dangling fashion. These setae formed part of a continuous series of setae on the anterior prothorax that coursed around the front of the larva as a setal fringe. On the sides of the larva, the anterior setal fringe joined with lateral setae to create an effective skirt of setae around the entire larva. On the prothorax lateral to the shield, four major spiculiferous setae comprised the remainder of the anterior fringe. These setae formed a diagonal line parallel to the anterolateral margin of the prothorax. The most medial of the four setae (MD1) was the shortest (120 microns) and approximately equal in size to D2 on the front of the shield. Posterolateral to MD1 on the same diagonal line was MSD1 (200 microns). MSD2 (170 microns) and L1 (170 microns) were the remaining setae of this diagonal group. The majority of the anterior fringe setae, especially shield setae and MD1, projected forwardly over the head and seemed to protect the retractable portion of the head which contained only tiny microscopic setae.

Two other setae of the lateral group, L2 (100 microns) and L3 (170 microns), were located close together on the lateral body fold of the prothorax, immediately beneath L1 and anterior to the small prothoracic spiracle. In the subventral area beneath the body fold were two additional very small setae (SV1 and SV2) and a lenticle. The larger SV1 (100 microns) was spiculiferous, while the smaller SV2 (30 microns) was non-spiculiferous and placed anterior to SV1. The lenticle was placed immediately above both setae. Downey (1979) referred to lenticles beneath the lateral setae as sublateral lenticles, but I prefer to designate them as subventral lenticles keeping with the terminology of the SV setal group to which they are closely associated.

*Mesothorax*: Striking double rows of major spiculiferous dorsal setae began on the mesothorax (Fig. 21) and continued posteriorly onto abdominal segments. These setae were the largest found on the body of the first instar and they formed a conspicuous part of the lateral body profile. D1 was medial in position and located adjacent to the mid-dorsal line. Supported by a large chalaza, D1 projected a gradual curve that moved upward, then backward and a little outward. D2 began slightly posterolateral to D1 and projected upward and strongly backward without any outward flare. On the mesothorax, D1 measured 420 microns in length and D2 nearly the same (400 microns). On subsequent segments, D2 became substantially shorter than D1.

On the extreme anterior margin of the mesothorax near the intersegmental groove (Fig. 21), there was a tiny microscopic seta (MD1). This seta averaged two microns in length and was usually located in the subdorsal region just anterior to the subdorsal lenticle. Its location near the intersegmental groove on all segments from the mesothorax to the ninth abdominal segment would indicate a proprioceptor function. The subdorsal lenticle of the mesothorax was uniformly present in all larvae examined and initiated a distinct row of subdorsal lenticles that continued to the seventh abdominal segment.

Lateral setae were all spiculiferous and formed a straight horizontal line on the lateral body fold (ridge). These setae were equidistant apart and designated L2, L3, and L1 from cephalad to caudad. The middle seta L3 was routinely the longest averaging 180 microns in length. The cephalad seta L2 was the next longest (160 microns) and the caudad seta L1 was shortest (110 microns). These respective lengths apply not only to the mesothorax, but also to the metathorax and abdominal segments one through seven. When viewed from above, each lateral seta was observed to project a slight gradual curve toward the rear of the larva. This curve was more pronounced on abdominal segments.

Beneath the lateral ridge in the subventral area, setae SV1 and SV2 and a small lenticle were found in a straight line. As on the prothorax, SV1 was larger and spiculiferous, while SV2 was non-spiculiferous and placed anterior to SV1.

*Metathorax*: The setal pattern of the metathorax was identical to that of the mesothorax in all respects. MD1, D1 and D2, subdorsal lenticle, L1, L2, L3, SV1 and SV2, and a subventral lenticle were all present. Setal lengths were also identical except for a minor shortening of D1 (400 microns) and a significant shortening of D2 (280 microns). These relative lengths remained essentially unchanged for the remainder of the segments which had setae of the dorsal group.

*Abdomen: First Segment (A-1)*: MD1, D1 and D2, subdorsal lenticle, L1, L2, L3, and SV1 were present. SV1 on A-1 and remaining abdominal segments was now non-spiculiferous and considerably shorter (60 microns) than SV1 of the thorax. SV2 and the subventral lenticle were absent. On the venter, a small microscopic seta MV3 (10-12 microns) was found adjacent to the mid-ventral line. Hinton (1946) described as many as three microscopic proprioceptors occurring on the venter of first instars with MV3 being the most ventral and the only one present on abdominal segments. Spiracles were present in a continuous line on segments A-1 through A-8. Each spiracle was placed slightly anterior to the midpoint of each segment.

*Second Segment (A-2)*: MD1, D1 and D2, subdorsal lenticle, L1, L2, L3, and SV1 were present. The venter contained a microscopic MV3 near the midline, plus an additional larger non-spiculiferous seta V1 (45 microns) just lateral to MV3. This medium-sized seta seemed to fill the gap on the bottom of the larva between the last pair of thoracic legs (metathorax) and the first pair of ventral prolegs (A-3). In this position V1 could serve either a tactile or proprioceptor role. A new lenticle appeared on this segment in the supraspiracular region. It was located nearly equidistant between the spiracle and the subdorsal lenticle, on occasion being slightly closer to the latter. The A-2 supraspiracular lenticle was absent in one larva.

*Third to Sixth Segment (A-3 to A-6)*: MV1, D1, and D2, subdorsal and supraspiracular lenticles, L1, L2, L3, SV1, and MV3 were present. A small subventral lenticle was also present on A-5 and A-6, just anterodorsal to SV1. Each ventral proleg bore two ventrolaterally-projecting smooth non-spiculiferous setae. The anterior proleg seta was somewhat smaller (30 microns) than the posterior seta (45 microns). It would appear that these setae served a proprioceptor role since they made contact with other prolegs and adjacent substrate during movement of the legs.

*Seventh Segment (A-7)*: MD1, D1, subdorsal lenticle, L1, L2, L3, SV1, and SV2, and MV3 were present. A number of changes in the pattern of the dorsal region were appreciated in this segment. D2 dropped out and was replaced by a dorsal lenticle on the posterior half of the segment. Also D1 and the subdorsal lenticle migrated slightly posteriorly. (An alternative interpretation would find the subdorsal lenticle having migrated to the position of the absent D2 and the supraspiracular lenticle in turn having migrated to the subdorsal region.) Both SV1 and SV2 were non-spiculiferous. On this segment, SV2 was located anterodorsal to SV1 instead of on a straight line as was seen in thoracic segments.

*Eighth Segment (A-8)*: MD1, D1, L1, L2, L3, SV1, and MV3 were present. D2 was absent and no lenticles were present. The lateral setae were present in the standard configuration, but the posterior seta L1 was reduced in size (80 microns).

*Ninth Segment (A-9)*: A narrow but distinct ninth abdominal segment was present and separated from the tenth segment by a visible intersegmental cleft (Fig. 24). This contrasted with the finding in some lycaenids (Plebejinae) where the two terminal segments were apparently fused. MD1, D1, L1, SV1, and MV3 were present on the narrow ninth segment. No lenticles were seen. Due to the size of the segment, the lateral series was reduced to a single seta, L1 (140 microns). Hinton (1946) designated the solitary A-9 lateral seta as L1.

*Tenth Segment (A-10) and Anal Shield*: A broad mid-dorsal anal shield was present. It was saddle-like in shape (220 x 110 microns) with the anterior portion parallel to the intersegmental cleft and the posterior portion rounded to fit into the terminal contour of the segment. Lateral poles of the shield were densely sclerotized and contained two side-by-side lenticles (Fig. 24). The central portion of the shield was minimally sclerotized, almost imperceptibly so. This created in some larvae the false appearance of two separate shields. No setae were found on the shield.

Three major spiculiferous setae were present on the lateral ridge of the last segment and appeared to be continuous with the lateral series of previous abdominal segments. Following the same convention used on other segments, these setae were designated L2, L3, and L1. Their respective lengths were 150, 200, and 250 microns. A pair of tufted setae was found on the suranal fold on a line slightly ventral to the spiculiferous lateral setae but still dorsal to the anal slit. They were somewhat shorter (120 microns) than lateral setae and their terminal tufts dangled posteriorly directly behind the anal opening. One of these tufted setae was medial to L1, resting next to the mid-dorsal line. The second was lateral to L1 and equidistant between L1 and L3. Hinton (1946) did not discuss setae of A-10, and the exact nature of the tufted setae is therefore quite speculative. (See discussion). For purposes of this study, tufted setae were simply described and left unlabeled.

The integument of the suranal and subanal folds was covered with a dense coat of epicuticular microspines (Fig. 24). These spines were directed posteriorly and averaged 15 microns in length, nearly seven times longer than the tubercles regularly found on the rest of the body. They were derived directly from the epicuticle and did not have separate chalazae or pinacula. On the suranal fold, integument spines covered the entire fold and advanced to the upper margin of the anal slit. On the opposite side of the slit, the dorsal portion of the subanal fold was completely spineless and marked with a series of very shallow longitudinal grooves. These grooves coursed caudoventrally for a distance of approximately 30 microns before being replaced by spines which covered the remainder of the subanal fold. The subanal fold also supported a horizontal row of continuous small setae that originated on the lateral portion of the anal proleg and then swept medially beneath the anal slit. This series consisted of six setae: four microsetae and two thorny setae. It was judged that all were derived from the anal proleg and comprised a unique anal proleg setal group. The first and most anterior of this series was a typical smooth microseta on the lateral aspect of the anal proleg. Second in line and immediately posterior to this was a thorny seta. Although these two setae were laterally-placed, they were not considered to be constituents of the subventral group. (See discussion.) These setae rested on a line below the subventral position of cephalad segments and they projected more posteriorly than laterally. Modification of the second seta clearly suggested its association with other thorny setae of this series. Following the second seta, the horizontal series continued around the postero-lateral margin of the proleg where a typical microseta was next in line. This was followed medially by another thorny seta which was slightly larger than the first. Finally, two more medial microsetae finished the series at the midline. (Two additional microsetae, not part of the subanal series, were located on the anteromedial portion of the anal proleg.) Right and left anal prolegs were bilaterally symmetrical. The subanal series of both prolegs together effectively formed a continuous uninterrupted series around the rear of the larva.

**Prolegs.** Crochets of the first instar ventral prolegs were arranged in a uniordinal mesoseries of eight crochets interrupted by a fleshy spatulate lobe (Fig. 13 M). The mesoseries was very strongly curved in a form of a mesopenellipse and separated into anterior and posterior groups of four crochets each. The anal proleg also had eight crochets, but interrupted into groups of six and two. The group of two was located posteromedially, while the group of six formed a series that swept anteromedial to anterolateral around the front of the anal proleg.

## SECOND INSTAR

**General.** The second instar maintained an onisciform shape (Figs. 4 & 26) and measured 2.5 mm in length immediately following the first molt and 5.0 mm in length just before the second molt. Head capsule width averaged .390 mm. The body was green in color with semi-glossy texture and a stripe pattern similar to the first instar (Fig. 4). A bold dorsal red stripe ran in the dorsal midline from the mesothorax to A-10 and was bordered on both sides by a solitary subdorsal white stripe. Ventral to this was a faint double row of oblique white dashes (two per segment) which slanted at a 30° angle oriented anterodorsal-posteroventral. On the lateral side of some larvae, there was an extra faint white line of broken horizontal dashes at the level of the spiracles. Finally, all larvae had a bold white stripe on the lateral ridge. The above description represents the fully-developed typical color pattern, but minor variations from one larva to another were common. Patterns of variation most often involved reduction in size of the dorsal red stripe, which was often restricted to the last few abdominal segments only, and reduction in intensity of the subdorsal oblique white dashes. An uncommon variant lacked red and white stripes except for the white line on the lateral ridge, leaving virtually a solid green larva. The color of the spiracles, chalazae, and lenticles was brown as before and the head capsule was very dark brown, nearly black.

**Integument**. A radical change occurred in the microanatomy of the integument between the first and second instar. The entire surface of the integument was now highly sculptured and organized into a distinctive pattern (Fig. 31). This pattern consisted of uniformly-spaced oval depressions dispersed over the epicuticular surface. Each oval contained a small hole in its center. The epicuticle surrounding each oval was non-depressed and in effect became an "elevated" ridge separating adjacent ovals. The typical oval depression averaged 15 microns in length, 10 microns in width, and 3 microns in depth. The central hole averaged 3 microns in diameter. This basic pattern of depressed oval integumental units was maintained in the remaining instars.

The geometrical pattern of large pits in the integument was identical to that of the first instar when compared segment by segment (Figs. 26 & 30). However, an additional feature that appeared in the second instar was the presence of furrows. Furrows were nothing more than simple folds in the integument and often originated near structures routinely depressed in the integument (e.g. prothoracic shield, integument pits). The only substantial furrow of note was a large one that began at the lateral wing (ala) of the depressed prothoracic shield and swept posteriorly through the prothorax, mesothorax, and metathorax at the subdorsal level (Fig. 27).

**Chaetotaxy of Body**. The addition of secondary setae to the larval body following the first instar dominated the chaetotaxy of the second and subsequent instars. Numerous secondary setae (25-30/segment) of the major spiculiferous type were now scattered over the body and, as a result, second instar larvae appeared quite "hairy" (Figs. 26 & 27). The pattern of primary setation from the first instar was now nearly obscured. The number of lenticles was likewise amplified and distributed irregularly over the body surface. Large primary setae of the dorsal group (D1 & D2) and lateral group (L1-3) could be picked out with some difficulty, but all other primary setae were unrecognizable. In the face of such huge numbers of secondary setae and additional lenticles, setal maps of second and subsequent instars were deemed useless. Only the prothoracic shield was spared invasion by secondary setae and may therefore prove important for comparative taxonomic studies. Like the integument pattern, the shape of the prothoracic shield changed radically between the first and second instar (Figs. 13J & 29). When viewed from above, the second instar shield was elongate (230 microns) and supported two separate pairs of lateral wings (alae). The anterior alae were longer, thinner, and more sharply pointed than the short and rounded posterior alae. Width of the shield at the anterior alae was 270 microns and width at the posterior alae was 120 microns. Anterior alar width was slightly greater than the axial length of the entire shield. Two pairs of primary setae were present on the alar arms. The filiform XD2 was situated on a button-like chalaza in a circular depression on the anterior alae. It was considerably longer (150 microns) than the first instar XD2 (40 microns). A pair of spiculiferous primary setae (SD1) was located on the posterior alae and measured nearly the same size (210 microns) as SD1 on the first instar shield. The lenticle seen in the upper portion of Figure 29 was associated with adjacent integument and did not reside on the shield proper.

Cranial setae and internal sculpturing of the spiracles were not studied in this instar.

## THIRD INSTAR

**General.** The third instar was onisciform in shape (Figs. 5 & 32) and measured 5.0 mm at the beginning of the instar and 8.0 mm at the end. Width of the head capsule averaged .632 mm. Body color was green with a distinct matt appearance and the stripe pattern was less striking than in previous instars (Fig. 5). A reduced and very faint red dorsal stripe occurred on the dorsal midline from the first to the eighth abdominal segment. This stripe was bordered on both sides by a faint white subdorsal stripe. In some individuals, both dorsal and subdorsal stripes were completely absent. Finally, a white stripe on the lateral ridge was uniformly present. This stripe was present in all instars, including those with variations in stripe pattern. The color of the spiracles, chalazae, lenticles, and head capsule was as before.

**Integument.** The basic pattern of depressed oval units was the same as in the previous instar (Figs. 36 & 31). One modification occurred. Epicuticular ridges situated between the oval depressions now supported very thin vertical partitions of chitinous material. These partitions averaged 3.5 microns in height and gave the integument a "honeycombed" or "chambered" appearance. This type of surface topography greatly reduced spectral reflectance.

The geometrical pattern of large integument pits (Figs. 33 & 36) was again the same as in the previous instars. Function of these pits was unknown and they seemed to show virtually no change from one instar to the next. Lastly, a large furrow in the integument was again found beginning at the anterior ala of the depressed prothoracic shield and curving posteriorly through the prothoracic segment.

**Spiracles.** Internal sculpturing of the spiracles (Fig. 34) differed significantly from the first instar. On the inside of the spiracular opening, flattened coral-like lobes of chitin extended parallel with spiracular walls for a short distance before terminating at the junction with endotrachea. Each flattened lobe resembled the palm of an extended hand bearing small spiny fingers. These fingerlike processes interconnected freely with adjacent lobes.

**Chaetotaxy of Body.** Secondary setation was amplified to 130-140 setae per segment. The larval body was extensively covered with spiculiferous secondary setae (Figs. 32 & 33) over the entire body except for the prothoracic shield, intersegmental clefts, and the venter. All setae were nearly uniform in size (300 microns) and the primary setal pattern was now totally lost. In relationship to total body size, body setae were now comparatively smaller than in previous instars.

Within the multisetose pattern, large numbers of lenticles were also scattered randomly over the body surface.

The prothoracic shield had the same configuration as that of the second instar (Figs 13K & 35). The shield measured 400 microns in length, 320 microns in width at the anterior alae, and 120 microns in width at the posterior alae. Filiform seta XD2 measured 230 microns and was again situated on a small button-like chalaza in a circular depression on the anterior alae. A pair of spiculiferous setae (160 microns) routinely appeared on the posterior half of the shield, but they were rarely arranged in a symmetrical position. They may have represented asymmetric SD1 setae, but it is also quite likely that they were random secondary setae that invaded the shield. Random unpaired lenticles were a frequent finding on the shield.

## FOURTH INSTAR

**General.** The fourth instar was onisciform in shape, and appeared to have a much broader prothoracic segment (Figs. 6 & 38). The widened lateral portions of the prothorax were frequently noticed wrapped around the head capsule and food substrate. This instar measured 8.0 mm at the beginning and 15.0 mm before entering prepupal quiescence. Just prior to pupating, the prepupal larva contracted considerably in length (9.0 mm) and rounded-up to form a broad axial arch (Fig. 7). The head capsule width averaged 1.05 mm. Body color was green with a distinct matt appearance similar to the third instar. On the whole, no stripes were present on the upper surface of the body and the solid green larva blended nicely with its foodplant. A dark green haemolymph vessel could be seen beneath the integument in the dorsal midline with exceptional larvae showing an extremely faint subdorsal white line bordering this haemolymph vessel. The lateral ridge uniformly contained a continuous white line, more often than not on the underside of the ridge (body fold) and not visible when viewed from the side. Color of the sclerotized parts (head capsule, chalazae, lenticles, spiracles) was as in previous instars. Spiracles in this instar were considerably bigger than before and demonstrated a brilliant white center surrounded by a brown spiracular ring.

**Integument.** The basic surface pattern was as in the previous instar except partitions between depressed units were now twice as high (8 microns). This greatly enhanced the "honeycombed" appearance of the integument (Fig. 43). When viewed directly from above, each surface unit delineated by the partitions appeared to have six sides. The tops of these partitions were wrinkled and wavy in nature and it was very difficult to observe into the depths of each unit because of the height of the partitions. Surface honeycombing effectively reduced spectral reflectance.

The geometrical pattern of large conical pits in the integument remained constant in this instar and throughout development. Although these pits showed essentially no change in position, they were significantly wider and structures at the bottom of the pits could now be visualized. Pits extended to a depth of 60-70 microns and their sides were covered with honeycombed integument. Each pit terminated with a round slightly convex button (20 microns) that occupied the floor of the pit. This button-like structure resembled some form of sensory placode. Its likely association with fixed segmental innervation may account for the invariable geometrical pattern of integument pits.

Integument furrows were now less evident on the prothorax since the shield was depressed to a much lesser degree into the integument.

**Spiracles**. Spiracles (Fig. 40) were very large (50 microns) and round. Internal sculpturing was elaborate and nearly filled the lumen leaving only a vertical slit-like opening (15 x 3 microns) in the center of the spiracle (Fig. 41). Detailed sculpturing was built upon the lobar pattern of the previous instar, but in this instance it was even more highly-branched and coral-like (staghorn coral). The chitinous meshwork was pure white in color.

**Chaetotaxy of Cranium**. Chaetotaxy of the fourth instar head capsule showed persistence of the primary cranial setal pattern with the addition of only a few new secondary setae. Very little new information was gained. Setation of the frontal, clypeal, adfrontal, genal, posterior, and vertex groups remained essentially unchanged from the first instar. The anterior group had added three new small microsetae in a vertical straight line medial to A1. The ocellar group was the most noticeably changed and a total of 14 microsetae now comprised this complex. As in the first instar, no seta was found anterior to the ocellar circlet, but six microsetae were now present within the circlet itself. One of these was presumed to be 01. A second group of eight microsetae occurred immediately posterior to the ocellar circlet, and one seta closely situated behind the sixth ocellus was slightly longer and presumed to be 02. There was a great deal of intraspecific variability within the ocellar complex. Some individuals did not even have the same number of ocellar setae on the two opposite halves of the cranial capsule. In the subocellar group, primary setae S01, S02, and S03 were still in an identical position to the first instar pattern. S03 was now a little longer. A new small microseta appeared between S01 and S03, plus another new microseta appeared immediately behind S03, making a total of five subocellar setae.

The labrum (Fig. 11 E) measured 420 microns in width and now had four pairs of setae in the medial group (M1-4) with M3 still being the longest (100 microns). Lateral group setae (L1-4) were nearly equal in size except for L2 on the anterolateral margin which was comparatively lengthened (50 microns) and measured approximately twice the size of other setae of the lateral group. The small puncture that was located in the first instar labral notch was not present in this instar.

The mandible (Fig. 11 F) measured 280 microns in length and now possessed a new type of biting edge. On the anterior margin of the occlusal plane, there were three small rounded incising teeth followed by a long knife-like cutting edge with fine serrations. This edge terminated laterally with a knob-like tooth. Two setae projected from the posterolateral mandibular margin.

Head capsule dehiscence occurred by cleavage along the adrontal sutures beginning at the cervical triangle and extending to the base of the mandibular insertion. Following this, the two epicranial halves rotated outwardly in the fashion of an opening book, thus creating a large dorsal exit hole.

**Chaetotaxy of Body**. Secondary setae of the spiculiferous type reached absolutely massive numbers on the body giving the larva a very dense "hairy" appearance (Figs. 6 & 38). Approximately 350 to 400 setae of this type were found on each segment. They uniformly averaged 250 microns in length and were comparatively shorter than their counterparts on the second and third instar. Numerous randomly arranged lenticles were also present. The primary setal pattern of the body was again totally obscured and dominated by secondary setosity. In fact, one wondered if primary setae truly even existed at this stage of development. Recognizable primary setae were limited to the head capsule and prothoracic shield.

A new element appeared on the body of the fourth instar. This was a specialized form of secondary seta resembling a tiny "mushroom" (Figs. 13 G & 42). These setae numbered approximately 100 per segment and were much smaller than spiculiferous secondary setae. Because of their dwarfed size and random distribution over the integument, they brought to mind a vision of "mushrooms in a forest". Individually, they ranged from 55 to 65 microns in height and averaged 34 microns in diameter. Each was borne on a separate chalaza and had approximately 50 thin blunt-tipped lobes projecting from the distal half. Collectively, the lobes projected upward and outward and gave the seta a globular contour. These setae were uniquely restricted to the integument of the last (fourth) instar.

The prothoracic shield maintained the same double-winged contour as seen in the second and third instar (Figs. 13 L & 39). The shield measured 540 microns in length, 400 microns in width at the anterior alae, and 170 microns in width at the posterior alae. In this instar, anterior alae were considerably broadened at their bases and merged together at the apex of the shield. When viewed from above, the shield resembled a large arrow pointing cephalad. Filiform seta XD2 (375 microns) was situated on a button-like chalaza in a circular depression at the lateral extremes of the anterior alae. Two or more asymmetric pairs of spiculiferous secondary setae and occasional lenticles often invaded the shield.

**Prolegs.** Crochets of the ventral proleg (Fig. 13N) were still arranged in an interrupted mesoseries, but with considerably more crochets than the first instar. The medial surface of each proleg contained approximately 60-70 crochets interrupted into two distinct groups (anterior and posterior) by a central spatulate lobe. Each crochet group had a multiseries of nine to ten rows of near equal-sized crochets. Such an arrangement was designated an interrupted mesomultiseries. On the lateral aspect of each proleg was a uniordinal lateroseries of five crochets alligned in a straight horizontal row. This lateroseries was not present in the first instar.

## PUPA

**General.** The obtect pupa of *L. epixanthe* was very short and plump in profile (Fig. 8). Length averaged 8.5 mm and ranged from 7.6 to 9.0 mm. Viewed from above, sides of the wing cases were straight except for a slight divergence at A-4 where the greatest width occurred (4.0 mm). Posteriorly, the abdomen was elliptical and well-rounded. Anteriorly, the thorax tapered very slightly in front of the wing bases, but terminated sharply truncate at the extreme front end of the pupa. Viewed from the side, the pupa looked double-humped. The abdomen was strongly arched and evenly rounded and reached a maximum height at A-4 (3.8 mm). The tiny last segment of the abdomen dropped off nearly perpendicular to the ventral surface which was flat throughout its entire length. A second prominent hump appeared on the mesothorax (3.5 mm) which was only slightly shorter than the abdominal hump at A-4. Anteriorly, the thorax sloped rapidly to the front of the pupa, while posteriorly the thoracic slope was gentle and formed a shallow curve at the point of junction with the abdomen. The head and cranial appendages were located on the ventral surface of the pupa as was a small semicircle of minute cremastral hooklets looped around the anal slit.

Immediately following the fourth molt, the great majority of pupae were uniformly solid green in color. Within a few hours, dark maculations had developed (Fig. 8). These maculations were organized more or less in series of longitudinal rows starting on the mid-dorsum where a fine black line extended from the prothorax to tenth abdominal segment. This line was punctuated by dark black maculations (one per segment) which were somewhat larger on abdominal segments. Lateral to the mid-dorsal line was a very faint, nearly obscure subdorsal row of brownish dots (one per segment). Below this was a supra-stigmatal row of dark black macules (2-3 per segment) beginning on the mesothorax and extending posteriorly. Finally, three more rows of weak black macules (one per segment) completed the maculation pattern. These rows occurred respectively in a line with abdominal spiracles, in a substigmatal row, and in a subventral row. The spiracles were colored pure white centrally and ringed with light brown. After five to six days, the wing cases became cream-colored and infuscated with light brown streaks. Eye, proboscis, and antennal cases were also infuscated with brown. Approximately, two days before eclosion, eye cases became dark black. The following day the thorax and abdomen also blackened. On the day of eclosion, the pupal skin was completely transparent and the imago visible beneath. Emergence of the adult was accomplished by a mid-dorsal split of the thoracic segments.

Approximately five percent of the pupae were uniform blackish-purple in color (deep wine color) without any trace of green or maculations. This was an unexpected polymorphism in pupal color. The purple morph demonstrated no detectable ultrastructural differences when compared with "typical" green pupae. Likewise, adults derived from the purple pupae showed no differentiating features.

**Integument.** The integument surface was covered with a fine reticulation of small elevated lines or ribs. These ribs varied in height from four to five microns and looked like fine delicate tracery when viewed on low magnification (Fig. 44). The rib network followed irregular courses and intersected frequently. At points of intersection, small doughnut-like papillae with plugged central pits interrupted the narrow ribs (Fig. 45). Integument between the ribs was divided into large angular polygons which contained numerous sensory verrucae and a specialized seta unique to the pupa (Fig. 45). (See chaetotaxy below). The sensory verrucae bore some resemblance to larval lenticles. They measured 15-20 microns in diameter and eight microns in height. Each had a circular exterior wall with a central dome-shaped membrane. A distinct groove separated the exterior wall from the central dome. These verrucae were heavily clustered around spiracles where ribbing was absent (Fig. 46).

**Spiracles.** The chitinous internal sculpturing of the spiracles was highly elaborate and coral-like, but quite unlike that seen in the larval instars (Fig. 47). Spiracular openings measured five microns in diameter and from their inner walls arose bluntly-rounded spatulate projections (15 x 5 microns) bearing fine chitinous spines. The lobulated sculpturing was white in color and filled the spiracular opening leaving only a vertical slit-like space communicating with the deeper tracheal system.

**Stridulatory Organ.** A well-developed stridulatory organ was located on the dorsal intersegmental membrane between the fifth and sixth abdominal segments and extended laterally to the level of the spiracles. The organ consisted of an opposing file and grating plate with a deep intersegmental cleft between (Fig. 48). The stridulating plate itself was located on the dorsal posterior membrane of A-5 and consisted of a narrow sclerotized band approximately 50 microns in width. The plate was characterized by small knob-like tubercles (2-3 microns in height) situated on fine transverse reticulations. The tubercles were aligned in loose transverse rows upon these reticulations. The file was located on the opposing anterior portion of A-6 and readily identified by its conspicuous sharp teeth. The recurved teeth were regularly spaced and easily imagined to grate against the opposing plate on A-5. Horizontal reticulations were also present on the file. A deep cleft representing the intersegmental fold plunged between the plate and file. Additional small tubercles and teeth, similar to those of the stridulatory organ, were also found loosely scattered on other intersegmental membranes of the abdomen not involved with sound production.

**Chaetotaxy.** A specialized trumpet-shaped seta, unique to the pupa, was found within the angulate polygons of the pupal integument (Figs. 13 H & 49). This seta was present over the entire body surface except for the wing, head, and cranial appendage cases. It was present on the venter, but numbers were somewhat reduced there. No useful taxonomic arrangement was detected in their placement and, to the naked eye, they appeared as dainty white pubescence. Individually, each seta measured 35 microns in height and terminated in an infundibular disc (funnel-shaped) averaging 40 microns in diameter. The disc was decorated with 15-20 small spines projecting from its peripheral margin. A few additional spines were located on the dorsal surface within the shallow "funnel". The base of the seta inserted in a central socket of a small cone-shaped pinaculum.

## DISCUSSION

Superficially, *L. epixanthe* would appear to be unique in comparison to all other species of North American *Lycaena*. This first-glance interpretation could be supported by its popularly known attributes of diminuitive size, unique habitat, and unusual foodplant. Indeed, it is the smallest of all Nearctic *Lycaena* and one of the few endemic butterflies solely restricted to bog habitats and the only butterfly utilizing cranberry. These features alone are totally unlike those of any other *Lycaena* and in this respect provide fascinating topics for study in evolutionary biology. Nevertheless, *epixanthe* remains an integral part of the lycaenine group. I found many close developmental and behavioral similarities between *epixanthe* and those published for other *Lycaena*. In many instances, generic homogeneity was striking and differences quite minor. It would appear that basic patterns of behavior and developmental morphology have been conserved within the genus.

Ecological factors that dictate the nature of bogs are both decisive for the occurrence of *epixanthe* and limit its distribution. The most important factor, of course, is the favorable environment for the growth of cranberry. The biology of the butterfly so closely parallels that of the foodplant that it is presumed that *epixanthe* is highly, or totally, restricted in its larval foodplant preference. Oviposition and successful rearing to date have occurred only on the diploid large cranberry *Vaccinium macrocarpon*, but it is suspected that the tetraploid small cranberry *Vaccinium oxycoccos* can also serve as a foodplant. This is especially true at the northern extent of the butterfly's range in the Canadian zone where *V. oxycoccos* replaces *V. macrocarpon* as the dominant cranberry species. In many instances, *V. oxycoccos* is the only cranberry species recorded in bogs where *epixanthe* has been taken (Bird, 1956; Masters, 1968; Maddox and Cannell, 1983). Broad areas of overlap also occur in the distribution of the two cranberry species, and it is possible the butterfly will be found to use both species locally or perhaps favor the more abundant one. To test the current understanding of *epixanthe*'s exclusive association with cranberry, rearing studies involving *V. oxycoccos* and several other members of the Ericaceae are being conducted.

Year after year, emergence of adult butterflies is timed to coincide with the cranberry flowering period. Adults are weak fliers and are seldom seen far from the plant. The hostplant is clearly the major nectar resource and *epixanthe* nectars almost exclusively on cranberry blossoms. On occasion, they also imbibe dew drops from the sphagnum surface and sedge blades, but it is the strong attraction for nectar that must account in part for the butterfly's constant presence around the foodplant. Nectaring on the larval foodplant may serve to not only replenish fluid losses, but also concentrate the population and facilitate courtship and pairing during the relatively short flightperiod.

Courtship is very similar among many species of *Lycaena*. As a generalization, perching behavior is the main method of mate-locating used by Nearctic male *Lycaena* (Scott, 1975). *Epixanthe* males perch on cranberry vines from which they fly out to investigate passing objects. Successful encounters are frequent since the butterfly population is densely concentrated and confined to the limits of the cranberry substrate within the bog. From time to time, flying males may encounter females in flight, but this would appear to be more accidental than intended patrolling behavior. Females mate shortly after emergence and mate thereafter infrequently. Most successful copulations occur in the mid-afternoon during peak male perching activity. The "rejection signal" utilized by unreceptive females of *L. arota* (Scott, 1974) and *L. xanthoides* (Scott and Opler, 1974) is also used by *epixanthe* females.

Dorsal wing surfaces of male *epixanthe* reflect brilliantly in the ultraviolet range. Since insect vision includes receptors in the ultraviolet spectrum, it is strongy suspected that UV reflectance is used by adult butterflies in intraspecific sexual communication. UV reflectance is the direct result of structural interference in specialized wing scales of the discal regions. Patterns of male reflectance are very similar among all *Lycaena* (Scott, 1973; Ferris, 1977). As perching males fly out to investigate passing females and vibrate their wings during courting, sex identification would seem unmistakable. The strongly reflective surfaces of the male wings could be likened to a beacon of light flashing "on" and "off".

The yellow/gray polymorphism for ventral wing color in the New Jersey populations appears to have no significance for sexual communication. Yellow is the most frequent (95%) color and also the type color for the species. The ventral yellow color loans its Greek derivative (*xanthos*=yellow) to the scientific name. Ventral gray color is the chief taxonomic character and distinguishing feature of the midwestern subspecies *L. e. michiganensis* (Rawson). The New Jersey low frequency (5%) gray morph is indistinguishable from the *michiganensis* holotype and a long series of the same subspecies examined at the U.S.N.M. Rawson (1948) was the first to recognize the rare New Jersey gray specimens, but he believed they were "aberrants" that appeared only periodically. In the author's study, the gray morph appeared routinely year after year, implying a balanced polymorphism. If this polymorphism proves to be genetically-controlled, as is likely, it may be important in establishing relationships between *epixanthe* subspecies and in determining sequences of post-glacial events.

Female *epixanthe* exhibit a unique technique when locating plants for oviposition. Uniformly, they select plants obscured by sedges around the perimeter of the bog or on hummocks within the center of the bog. After landing on the sedges, they walk down and through the sedge tangles to reach cranberry plants hidden below at sites they would be unable to fly to directly. Cook and Watson (1908) similarly noted that females are "almost out of site among the vines" when ovipositing.

Fecundity is a key factor to evolutionary success. Fresh-caught *epixanthe* females yield on the average 28 ova/female in confinement. This is slightly greater than the number found by Newcomb (1909) for the closely-related congener *L. dorcas* (11.5-21 ova/female). Egg production in confinement obviously depends among other things on the method and conditions of confinement and the ages of females confined. Cook and Watson (1908) reported on two *epixanthe* females which yielded 40 and 42 ova respectively when confined immediately after mating, probably reflecting a more accurate representation of the total egg numbers capable of being produced. Some isolated bogs in upland New York have *epixanthe* populations estimated to contain as few as 50-100 adult individuals per yearly generation (Shapiro, 1974). Using these figures as an example, if 100 adults were to successfully mate and realize maximal reproductive capacity, the next generation would start with 2,000 potential individuals. If an average of only 100 individuals again survives to adulthood, we then have an approximation of the large reproductive excess needed for colony survival.

Ova of *epixanthe* are typically lycaenine. The outer chorion is highly reticulated and honeycombed in appearance, and frequently covered with streamers of chorionic secretion. This geometric pattern is uniformly similar to ova of other Nearctic *Lycaena*, particularly congeners of the same subgenus *Epidemia* (Ferris, 1977; Downey and Allyn 1981). Surprisingly among the *Epidemia* there are no appreciable differences in ova size, despite differences in size of adult butterflies. The dimensions of *epixanthe* ova are nearly identical to those published for *dorcas* (Newcomb, 1911), *helloides* (Coolidge, 1924), and *nivalis* (Newcomer, 1911). Differences in size of adults are most certainly accounted for during larval development through the number of genetically-prescribed instars and the condition of the hostplant.

The micropylar region of *epixanthe* ova has a notable configuration that, for all intensive purposes, is indistinguishable from other Nearctic *Lycaena* found in Downey and Allyn's (1981) survey. Some intraspecific variability exists in the number of petal-shaped cells of the micropylar region, but this is common within the *Epidemia* (Ferris, 1977). *Epixanthe* has four to five cells in the rosette, while *dorcas* and *helloides* usually have five to six. The micropyle itself is a small pentagonal depression with five tiny holes at the apices. The same arrangement is shown for *dorcas* by Miller and Brown (1979, Fig. 58) and it is suspected that all *Lycaena* share this pattern. Miller and Brown's (1979, Fig. 57) SEM of *helloides* micropyle is presented by the authors in proof that *helloides* is taxonomically different, but their ovum is so excessively coated with gold/palladium (or possibly vitelline fluid) that the micropyle holes are completely buried and obscured. This is unfortunately interpreted by the authors as a unique taxonomic character.

Beyond the micropylar region, the highly convoluted *epixanthe* chorion encloses a labyrinth of continuous airspace which covers the entire egg surface except for the flat bottom. This constant gas film around the ovum is predicted to serve as a plastron or physical gill allowing gas exchange to occur when the ovum is submerged in water. Bog habitat is often temporarily flooded in late winter and early spring when snows melt and heavy rains set in. At these times, the bog floor may be submerged for several days. Additionally, special structural features of the cranberry leaf guarantee that ova will be covered with water droplets following rains at any time during the year. The cranberry leaf is characterized by its small size, resinous upper surface, and strongly revolute or inrolled lateral margins. Rain water rolls off the hydrophobic upper leaf surface and is easily trapped on the lower surface in the depression between revolute margins. I have seen *epixanthe* ova covered with raindrops retained for two to three days after a routine rainshower. Because of this, plastronic respiration is clearly implicated. To test the hypothesis, further studies are needed to compare the total area of plastronic pores ($u^2$) with the weight (mg) of the diapausing larva within the egg (Hinton, 1969). In this way only, can plastronic respiration be proven efficient for oxygen requirements of the larva. Plastronic respiration has been proposed for several lycaenids (Downey and Allyn, 1981), but Hinton's formula-of-proof has not as yet been applied to any lycaenid species. Further studies with *epixanthe* in this regard are pending.

It would be expected that ova that have solved the problem of respiration under wet conditions would also be faced with the problem of water loss under dry conditons. Plastronic pores offer little resistance against dessication and would seem to be detrimental in hot dry weather, especially for small ova with large surface area-to-volume ratios. Some insects have solved the water loss problem by evolving plastron-bearing horns, e.g. *Drosophila*, and maintaining impermeability over the rest of the chorion (Hinton, 1969). In eggs that lack plastron-bearing horns, the same effect may be achieved by having only a small area of the inner chorion permeable to respiratory gases (*loc. cit.*). In *epixanthe* ova, the thick inner chorion (4 microns) is uniformly solid and most likely impermeable except for a small circular area on the dorsum of the egg surrounding the micropylar region. Here the inner chorion is filled with clustered small spongiform air cells that occupy the entire thickness of the inner chorion but do not perforate its surface. If the rest of the solid inner chorion is impermeable as it appears to be, water loss could then be confined to the small spongy area on the dorsum of the egg. In this way, plastronic respiration could function when submerged and water loss could be minimized when dry.

In addition to egg design, *epixanthe*'s microhabitat preference for the cool moist sphagnum carpets on the bog floor undoubtedly also plays a major role in reducing fluid loss. In an experiment outlined above, a balance was indicated between environmental moisture and survival of diapausing larvae: when hostplant leaves were clipped and removed from their microenvironment, they quickly dessicated as did the diapausing larvae within the attached eggs. Such was the problem encountered by Cook and Watson (1908) in the summer of 1907 which precluded their success in rearing *epixanthe* larvae. Thus both egg design and microhabitat contribute to larval survival.

Outer egg chorions of Holarctic *L. phlaeas;* Ethiopian *L. orus* and *clarki;* and Indo-Australian *L. salustius, feredayi,* and *boldenarum* display a rather simple bold cellular pattern with very large chorionic cells and few chorionic ridges (Downey and Allyn, 1981; Clark and Dickson, 1971; Gibbs, 1980). Such a simple chorionic pattern is far less convoluted than ova of Nearctic *Lycaena* and would appear to enclose a significantly smaller intrachorionic airspace. The above species do not diapause as ova and their ovum phase is very brief. It is attractive to speculate that their simple chorionic pattern is related to a different life history strategy and lack of a need for plastronic respiration. By comparison, a large proportion of Nearctic *Lycaena* diapause as ova and have highly-reticulated, finely-cellular chorions. Plastronic respiration would be of decided value for this group during diapause.

Following diapause, *epixanthe* reaches maturity through a four-instar larval development. Four instars appears to be the typical developmental pattern for most of the Lycaenidae, although an additional fifth instar is reported for some larger lycaenids including some lycaenines. Partial larval descriptions are available for several North American *Lycaena* species, but complete life histories are noticeably few in number. Four instars are reported for *nivalis* (Newcomer, 1911), but five instars for *dorcas* (Newcomb, 1911), *helloides* (Coolidge, 1924), *phlaeas* (Scudder, 1889), and *xanthoides* (Comstock and Dammers, 1935b). New Zealand lycaenines *L. salustius, feredayi,* and *boldenarum* are recorded with four instars (Gibbs, 1980). It would be desirable to compare the larval phases of more *Lycaena* species to determine if a certain prototype adult size (mass) requires a level of vegetative growth that can only be attained through the addition of another larval instar. Caution should be exercised in determining the number of larval instars. Downey and Allyn (1979) have previously pointed out discrepancies in the literature regarding the number of instars of plebejine species. This is a common error and many older studies should be re-examined. The marked differences in trunk size of early and late first instars may be easily confused as two separate larval instars, especially if several larvae are confined together. A reliable index for determining instar numbers is the width of the larval head capsule (Dyar, 1890). The head capsule is heavily sclerotized and relatively fixed in size for each instar. The width is progressively larger in each successive instar and the number of instars is easily determined by the geometrical progression.

The value of complete and accurate life history studies is well demonstrated by Clark and Dickson's (1971) example of two closely-related South African lycaenines which were originally thought to be one species. Primarily on the basis of distributional and larval development differences, a new species *L. clarki* Dickson was discriminated from the older species *L. orus* (Cramer). *Clarki* is slightly larger and matures through a five-instar development, while *orus* is smaller and requires only four instars. In this instance, the fifth instar of *clarki* is an identical morphologic version of the fourth instar except for size. No new setal elements or arrangements appear in the fifth instar. Likewise for Nearctic *Lycaena,* the fifth larval instar seems to be an exact, but larger copy of the fourth instar. Such a conclusion is well demonstrated by use of the specialized mushroom-like secondary seta which serves as a unique marker for maturity of *Lycaena* larvae. This seta occurs in the fourth and last instar of *epixanthe* and *nivalis*, while in *dorcas* and *helloides* the same seta is present in both fourth and fifth instars. In all these examples, the mature larval pattern is already present by the fourth instar. Such data suggest that the four-instar development is the basic lycaenid pattern and evolutionary changes toward larger adult size are accomodated by adding another identical instar.

*Epixanthe* larvae in all phases are well-designed for concealment within the cranberry bog environment. An ontogenetic progression of programmed defenses help protect the larvae during development. Young larvae are present in the spring before new cranberry shoots appear and feed totally concealed on the undersurfaces of older evergreen leaves. They are boldly marked with red dorsal stripes which effectively camouflage them on the anthocyanin-tinged vegetation of early spring. This protective red-on-green pattern of early instars is found frequently among lycaenid larvae and correlates well with colors of the hostplant during early larval development. Other red-on-green lycaenid examples that immediately come to mind are *L. nivalis* (Newcomer, 1911), *Plebejus (Agraides) aquilo* (Day and Jackson, 1980), and *Callophrys (Incisalia) augustinus* and *polios* (Ziegler, 1953). Later instars are generally present about the time new cranberry shoots unfurl and begin to grow rapidly. Anthocyanin pigments disappear from the cranberry about this time and the late larvae feed in exposed positions on the new green shoots. These instars, for the most part, have green non-striped bodies.

In accordance with exposed feeding, the body surface of later instars has a subdued matt appearance which provides considerably less spectral reflectance than the semi-gloss surface of earlier instars. The morphological basis of this phenomenon is found in the ultrastructure of the larval integument. The first instar integument is relatively flat and smooth, interrupted only by small widely-spaced microtubercles. Spectral reflectance of this instar is high, since a large proportion of the integument is oriented in one plane. Following the first instar, a radical change in the microanatomy of the integument takes place. The fundamental pattern switches to a geometrical arrangement of large oval depressions in the epicuticle. This type of sculpturing is known as the "macro"-type (Byers and Hinks, 1973). Each "macro" surface unit is the product of a single underlying hypodermal cell. When surface units are smooth and oriented to provide a large reflecting area, as they are in the second instar, the epicuticle appears shiny or semi-glossy. Thus both the first and second instars have a relatively bright body surface, although they are ultrastructurally different. Their behavioral concealment on leaf undersurfaces and camouflaged markings reduce the value of adaptive modifications to the larval integument of early instars. On the other hand, a matt appearance with reduced reflection would appear to have an adaptive value in making the exposed older larvae less conspicuous. Reduction of spectral reflectance in later instars is accomplished by the addition of thin vertical partitions around each epicuticular "macro" unit giving the integument a honeycombed appearance. These partitions, absent in the second instar, are extremely effective in light scattering and diffusion. Byers and Hinks (1973, Fig. 12), in their ultrastructural survey of the lepidopterous larval integument depict an example of the integument of *L.hyllus (=thoe).* The similarities to *epixanthe* are immediately obvious. After studying several additional scanning micrographs kindly loaned by J. R. Byers (pers. com.), it is concluded that the larval integument of *hyllus* and *epixanthe* are ultrastructurally identical. It is suspected that this type of integument may be universal within *Lycaena.* Recent integument SEM's from New Zealand (Gibbs, 1980) of larval *L. feredayi* and *boldenarum* show identical integument morphology with *hyllus* and *epixanthe.* This tends to strengthen the argument for universality.

A great deal of emphasis in this study is placed on the ultrastructure and chaetotaxy of the first instar *epixanthe* larva. There is no thorough treatment of any *Lycaena* species on this subject in the literature. The importance of the first instar larva comes from the widespread belief among larval morphologists that this instar is a specialized embryonic stage reflecting primitive characters of an archetype larva. Consequently, by comparing the arrangement of first instar larval characters of many species within a given taxon, patterns of relatedness and divergence may be implied. The paucity of chaetotaxy studies within Lycaenidae is due in large part to the minute size of lycaenid larvae and the limits of resolution by light microscopy. Setal mapping is greatly facilitated by use of the scanning electron microscope and this instrument should become the standard for detailed studies of first instar lycaenids.

The overall configuration of the *epixanthe* first instar cranium differs only in minor detail from the few other lycaenids studied. Lateral adfrontal sutures extend dorsally to the cervical musculature without meeting in the midline, thereby leaving the frons open. While this condition is uncommon in lycaenids, it is not unknown. Scudder (1889, Pl. 79, Figs. 27 &42) found the head capsule of *Callophrys (Mitoura) gryneus* and *C. (Incisalia) irus* with an open frons. Curiously, he missed the open frons of the solitary *epixanthe* larva he dissected. Appendages of the *epixanthe* cranium are very much like those of *Everes comyntas* and *Leptotes cassius theonus* (Lawrence and Downey, 1966; Downey and Allyn, 1979). The *epixanthe* mandible has five teeth instead of the six to seven teeth found on the plebejine mandible and the *epixanthe* labral puncture sits centrally in the labral notch instead of between setae M1 and M3. Some minor differences also exist in the number of setae on the basistipes, but the most interesting difference is found in the sculpturing of the hypopharynx. The *epixanthe* hypopharynx consists of a smooth spineless lingula and a midline trough along the floor of the mouth. The latter is flanked on both sides by fleshy lobes of the paraglossae which bear tiny microspines paired in twos. The plebejine hypopharynx, on the other hand, is spiny over its entire surface and spines are not limited to the paraglossae. As suggested by this small comparison, the arrangement of hypopharyngeal spines could eventually prove to be of taxonomic value. This concept was first promoted by

Downey and Allyn (1979) and awaits further comparative studies.

Chaetotaxy of the *epixanthe* cranium is quite simplified. It too resembles the aforementioned plebejines with minor modifications. Hinton (1946) states that a broad uniformity of lepidopteran cranial setae is found throughout the order and a general primitive pattern is preserved. He feels that few modifications of the primitive pattern have occurred during adaptive radiation, plus adjustments that have taken place generally did so through slight changes in position and relative lengths rather than through acquisition of new setae. Because of general uniformity throughout the order, cranial chaetotaxy is of little value in separating families. However, slight minor differences become important in determining genera and species. Cranial setae of *epixanthe* fall roughly into two groups: 1) long tactile setae clustered anteriorly on the head capsule which project forward ready to contact objects in front of the larva, 2) short proprioceptors scattered posteriorly which provide information regarding head position when deeply retracted into the prothorax. Each setal group on the retractable portion of the head is significantly reduced in length and number. All setae of this area are microscopic in size and setae A3, O2, O3, L1, P2, and V3 are absent. This condition represents a somewhat greater modification than that found on the retractable head capsule of *E. comyntas* and *L. cassius*.

Setal arrangement on the thorax and abdomen shows more variability throughout the order than cranial setae and, as such, becomes a useful tool for distinguishing species, genera, and even families (Hinton, 1946). Before discussing chaetotaxy of the *epixanthe* larval body, a short introduction seems in order. Three classes of setae (primary, subprimary, secondary) are recognized on the lepidopterous larval body. Primary setae are those that are present on the first instar and remain essentially unchanged through subsequent instars. These setae are the dominant features of the first instar and are thought to represent primitive setae derived from an archetype larva (*loc. cit.*). In this line of thought, closely-related species are expected to show some degree of setal homogeneity and unrelated species to show divergent setal patterns. Secondary setae are not present on the first instar, but make their appearance on the second and later instars. In evolutionary terms, these setae are thought to be more recently acquired in the history of the organism and represent responses to varying environments. In certain families like Lycaenidae, they tend to be very numerous and sometimes highly modified in appearance. On certain occasions, modified secondary setae can become so distinctive as to effectively serve as a marker for a given group (e. g. "mushroom" seta of late *Lycaena* larvae). Subprimary setae are more common in primitive families and by definition are not present on the first instar, but appear in subsequent instars as new setae situated in constant positions very much like primary setae. They are always few in number. There is a tendency for certain setae (L3) which are subprimary in primitive families to appear regularly in the first instar of more highly specialized families (e.g. Lycaenidae). As such, they should be treated as primary setae and mapped accordingly.

On the first instar *epixanthe* larva, five different types of primary setae occur. Long spiculiferous tactile setae and tiny proprioceptive microsetae are by far the most common. Their large numbers attest to the important sensory roles they perform. They are arranged in recognizable patterns on the body surface and are convenient characters for comparative mapping. Lenticles likewise are a prominent feature of the first instar integument. They are given various names by other workers (annuli, cornicula, crateriform papillae, hairless tubercles, perforated cupolas) and appear to serve a glandular or sensory function. While they are not derived from setae, they do have an orderly arrangement on the first instar and can be mapped along with primary setae.

In contrast to the cranium, the setal map of *epixanthe* thorax and abdomen is considerably different from that of the published Plebejinae (Lawrence and Downey, 1966; Downey and Allyn, 1979). Unfortunately, no setal maps of other *Lycaena* species are available for comparison. Very few descriptions of first instar *Lycaena* exist in the literature, e.g. *phlaeas* (Scudder, 1889), *hyllus (loc. cit.), nivalis* (Newcomer, 1911), *dorcas* (Newcomb, 1911), *helloides* (Coolidge, 1924), *xanthoides* (Comstock and Dammers, 1935b), *orus* (Clark and Dickson, 1971), *clarki (loc. cit.*), and *feredayi* (Gibbs, 1980). All are brief and poor in setal descriptions. The only broad generalization that can be drawn is the uniform presence of prominent double rows of dorsal setae, D1 and D2, and a skirt of prominent lateral setae. These setal groups are not unique to *Lycaena*, but common throughout the Lycaenidae. Most interestingly, the row of D2 setae terminates at the sixth abdominal segment in *epixanthe, dorcas, nivalis, phlaeas, orus*, and *feredayi*. These butterflies represent a distributional spectrum from Nearctic, Holarctic, Ethiopian, and Indo-Australian realms. The precise uniformity of their dorsal setae suggests that primary dorsal setae have changed little from proto-*Lycaena*. The only species with which more than a superficial comparison could be made with *epixanthe* is the South African *L. orus* and the New Zealand *L. feredayi*. Clark and Dickson (1971, Pl. 47) depict the entire life history of *orus* in a detailed hand-colored composite. Gibbs (1980, Pl. 163) includes an exquisite color photograph of *feredayi* first instar. Setal descriptions are absent in both texts, yet the graphic resemblance to *epixanthe* stands out immediately. Major setal groups, anal shields, and subdorsal and supraspiracular lenticles appear nearly identical to those of *epixanthe*. Details of the cranium, prothoracic shield, and venter are lacking, but the degree of homogeneity thus far determined is noteworthy. During geologic history, the North American continental plate and the conjoined Antarctic-

Australian plates (with New Zealand still attached) are believed to have completed separation from the African plate in the late Cretaceous approximately 100 million years ago. In view of this, the resemblance of *orus, feredayi,* and *epixanthe* first instars attests to the profound tendency to preserve archetype characters in first instar larvae of the genus.

The *epixanthe* prothoracic shield is a distinctive anatomic structure which awaits comparison with other *Lycaena* species and may be taxonomically useful. The *epixanthe* shield supports four sets of primary setae and a pair of lenticles in the first instar. Most of the setae are tactile in type, but a unique filiform seta, XD2, differs from the others. It originates from a depressed puncture-like opening in the rear of the shield and vibrates strongly in air currents. Hinton (1946) in his study of moth larvae routinely found a puncture, XDa, near the base of XD2 and often used this puncture to establish the certainty of XD2 identification. It is easy to speculate this puncture may have been incorporated into the base of XD2 in higher specialized families like Lycaenidae. XD2 is the only shield seta that can be traced completely through *epixanthe* larval ontogeny. In later instars, intense secondary setosity covers the entire larva and XD2 becomes the only clearly-identifiable primary seta remaining on the body. Lawrence and Downey (1966) were able to trace two shield setae, XD2 and SD1, through *E. comyntas* larval ontogeny. Following *epixanthe*'s first molt, a radical change takes place in configuration of the shield, analogous to the change observed in integument sculpturing. A new transformed shield makes its appearance in the second instar and from there on fundamentally remains the same in subsequent instars. It is quite clear that many characters of the first stage of larval life (e.g. integument, shield, setation, spiracles, proleg crochets) are distinctly differentiated from remaining larval stages.

Setation of the anterior and posterior extremes of the lycaenid larval body are unique areas that may also prove to be taxonomically useful. In *epixanthe*, the anterior margin of the first instar prothorax contains a row of long tactile setae that together with shield setae project forwardly over the larval head. This condition is common within lycaenids where the dorsal region of the retractable head lacks its own tactile setae. Using Hinton convention, Downey and Allyn (1979) designated the prothoracic setae as MD1, MSD1, MSD2, and L1. Although the first three setae bear a nomenclatorial "M", they are not microsetae in the true sense. In *epixanthe*, these setae are all long and tactile. Nevertheless, a microsetal origin cannot be ruled out. Ultrastructural studies of first instar *Brephidium pseudofea* (Morrison) show that MD1 in this species is small and microseta-like (Wright, unpubd. data) which is the first evidence these setae may have a microsetal derivation. Hinton (1946) states that MD1 is not present on the thorax, yet he emphasized that various setae on the body of higher specialized families may undergo elongation, multiplication, fusion, and other assorted modifications. Whatever their origin, it is clear that MD1 and the MSD group evolved on the lycaenid prothorax to form a protective fringe of tactile setae over the head and neck.

At the posterior end of the larval body, *epixanthe*'s ninth and tenth abdominal segments are distinctly separate and marked by a clearly visible intersegmental cleft. This is in contrast to the terminal portion of the plebejines *Everes comyntas* and *Leptotes cassius* where A-9 and A-10 appear fused as one segment (Lawrence and Downey, 1966; Downey and Allyn, 1979). *Epixanthe*'s narrow ninth segment is reduced in setation as well as size. MD1, D1, SV1, and MV3 are present on the contracted segment and only one lateral seta occurs. Hinton (1946) correctly recognized that Rhopalocera usually have only one lateral seta on the ninth segment (L1). *Epixanthe*'s tenth segment has three major lateral setae on the body fold (L1-3) which reside in a continuous line with lateral setae of previous abdominal segments. On a line slightly ventral to these setae, directed posteriorly, are two tufted setae whose terminal ends dangle over the anal opening. These setae are easily differentiated from lateral setae by size and appearance. Downey and Allyn (1979) in their study of *L. cassius* incorporated these tufted setae into the lateral setal group of fused A9-10. In doing so, they derived a total count of six lateral setae (three for A-9 and three for A-10). Some of their A-9 setae are clearly in the province of A-10 and I have reason to believe this setal arrangement is incorrect. It seems quite improbable that a full complement of A-9 lateral setae (L1-3) exists on the fused A9-10 plebejine segment. An equally-balanced fusion of two complete anatomical units would be a rarity. A much more logical event during the course of evolution would be an initial attenuation or reduction of one or another segment, followed by its fusion with a neighbor segment or complete disappearance. Since many lepidopteran families, and especially lycaenines, have a small A-9 segment with reduced setation, the course of plebejine evolution could not have been much different. It would seem logical that the plebejine A-9 fused with A-10 only after it was initially diminished in size. In this analysis, the lycaenid A-9 may be regarded as an evolutionary "degenerate" unit and A-10 as a very highly-specialized unit. I would recommend that any system of setal names used to describe the terminal segment(s) of lycaenines and plebejines employ only one A-9 lateral seta.

The *epixanthe* tenth abdominal segment also has a dorsal (anal) shield and a row of unique subanal setae. The shield is very weakly sclerotized and recognized only by its slightly depressed nature. No setae originate from the shield, but two lenticles appear on each lateral margin. *Epixanthe*'s shield is identical to that pictured for the South African *L. orus* (Clark and Dickson, 1971) and *L. feredayi* from New Zealand (Gibbs, 1980). All in all, judging from its sparse decoration, the lycaenine anal shield will probably prove to be of little taxonomic value in comparative studies. A more interesting region of the tenth segment is the subanal fold where a row of small setae sweeps beneath the anal opening. Six setae are found on each half of the segment, beginning on the lateral aspect of the anal proleg and coursing to the midline beneath the anal slit. The entire row is derived from anal proleg setae. It was originally thought that two of the setae on the lateral aspect of the proleg represented subventral setae SV1 and SV2, but it is now believed that SV1 and SV2 don't occur on A-10. The two setae in question are situated considerably below the subventral line and aligned with ventral proleg microsetae of previous segments. Furthermore, one seta is thorny in configuration unlike any seta of the SV group. Other thorny setae are found in the subanal row which clearly attests to the relatedness of the entire subanal series.

The architecture of the terminal portion of the tenth segment appears to be designed to facilitate expulsion of frass (Downey, pers. com.). It is not uncommon when observing live larvae to see expelled frass pellets momentarily "hang-up" behind the anus and then drop free several seconds later. The row of subanal setae may serve as a ledge to catch frass pellets and prevent them from lodging beneath the body. Similarly, the tufted setae on the suranal fold may prevent frass from tumbling over the top of the body when the larva is inclined head-down. In this way, frass pellets may be safely guided away from the body. Newcomb (1911) in his description of first instar *dorcas* larvae referred to "two small branched spines project(ing) caudad from the last segment, just below the anal opening." These "branched spines" may very well be identical to the thorny setae found in the subanal row of *epixanthe*. This region is fascinating and future comparative studies of lycaenid larvae should include its examination.

The value of certain inconspicuous minor larval characters remains unknown, but the effort to examine them may be worthwhile. Some regional areas with promise are the spiracles and ventral prolegs. The internal sculpturing of larval spiracles is very elaborate and detailed. Sieve-like patterns within the spiracular lumina are presumed to prevent dust, foreign bodies, parasites, and even water from entering the tracheal system. At this time, very little information is available regarding spiracle microanatomy of lycaenid larvae. They are readily accessible to study by SEM and their changing geometrical designs during ontogeny seem to offer a fertile field for investigation. Lastly, the ventral prolegs are frequently overlooked in descriptive works, but they too are easily studied with SEM. Each first instar *epixanthe* ventral proleg has a uniordinal mesoseries of eight crochets divided into two equal groups by a median fleshy lobe. An interrupted mesoseries of this type is diagnostic of the Lycaenidae, but it is now known that the number and size of first instar crochets may vary between species. For example, eight crochets occur on the *epixanthe* proleg, but only four are found on the prolegs of the plebejines *E. comyntas* and *L. cassius*. (See also discussion of later instar prolegs below.)

In concluding the discussion of the *epixanthe* first instar, it is important to point out again that the first stage of larval life is morphologically differentiated from the remaining stages. Changes in some larval characters at the first molt are so profound that it is sometimes difficult to imagine the initial two instars represent the same species. However, after the first molt, most larval characters remain fundamentally unchanged and subsequent molts thereafter yield only minor modifications. This pronounced transformation of the primitive first instar to the second instar is viewed as a major step in ontogenetic progression. Changes that occur at this point were described by Scudder (1889) as "hypermetamorphosis". In the true sense of the word, larval metamorphosis is represented by all larval stages taken together. Yet within the general framework of larval metamorphosis, "hypermetamorphosis" may be looked upon as a specialized form of change that transforms the primitive archetype larva into the "advanced" later larva which enjoys all the adaptive characters gained through evolution.

After the first instar, patterns of setosity on the larval body tend toward greater and greater numbers of secondary setae. Eventually, the later instars become so densely covered with secondary setae that the original primary setal pattern is totally obscured and perhaps even non-existent. Seta XD2 on the prothoracic shield is the only seta of later instars that can be positively identified as a primary seta.

Near the end of larval ontogeny at the beginning of the fourth instar, a new specialized form of modified secondary seta makes its appearance for the first time. This seta resembles a tiny white mushroom and is considerably smaller than the major spiculiferous setae. It is scattered over the larval integument in typical secondary setal fashion, reaching numbers of 55-65 per segment. Its ultrastructure was unknown until it was included as an incidental finding on the cuticle of *L. hyllus (=thoe)* in Byers and Hinks' (1973) SEM survey of lepidopterous larval integument. This seta is identical in both *epixanthe* and *hyllus* and it is now known to occur throughout the genus *Lycaena*. It is variously described in older literature as white granulations, wartlets, vibrissae, ovoid tubercles, bulbous processes, egg-shaped processes, globe-like setae, pom-pom setae, and mushroom-shaped appendages. To date, the unique seta has not been found in any other lycaenid genera and it is virtually certain that it is an effective marker for mature *Lycaena* larvae. The following *Lycaena* species have been recorded with the seta: *arota* (Comstock, 1928), *xanthoides* (Comstock and Dammers, 1935b), *editha* (Scott, 1979), *hyllus* (Scudder, 1893), *heteronea* (Williams, 1910), *dorcas* (Newcomb, 1911), *helloides* (Coolidge, 1924; Comstock, 1929), *nivalis* (Newcomer, 1911), *hermes* (Comstock and Dammers, 1935a), *dispar* (Whalley, 1979), *orus*

(Clark and Dickson, 1971), *clarki (loc. cit.), feredayi* (Gibbs, 1980), *salustius* (*loc. cit.*), and *rauparaha (loc. cit.)*. No mention of this seta could be found in the vast literature for the widely-distributed *phlaeas*, which is a common butterfly that has been reared countless times without record of the unique seta. I was kindly loaned a *phlaeas* pupal specimen from the New York State Museum, Albany, NY, collected over one hundred years ago by past State Entomologist Jos. Lintner. The last instar exuvia was recovered from the loosely-constructed hibernaria surrounding the pupa. Under SEM examination, the larval setae were still clearly intact and visible on the century-old exuvia. It can now be positively stated that mature *phlaeas* larvae possess the specialized mushroom-shaped secondary seta.

Mature *epixanthe* larvae have a broad arrow-shaped prothoracic shield, quite differentiated from the first instar shield. This configuration is apparently uniform within the *Lycaena*, as it is shared by mature larvae of *arota* (Dyar, 1891), *xanthoides* (Comstock and Dammers, 1935b), *nivalis* (Newcomer, 1911), *hermes* (Comstock and Dammers, 1935a), *orus* (Clark and Dickson, 1971), *clarki (loc. cit.), salustius* (Gibbs, 1980), *rauparaha (loc. cit.), feredayi (loc. cit.)*, and *boldenarum (loc. cit.)*. Setation of the large mature shield is considerably reduced and XD2 is the only primary seta found in *epixanthe*. This seta is also commonly present on the mature shield of plebejines. Curiously, in New Zealand *Lycaena*, XD2 is present on the mature shield of *feredayi*, but absent on *boldenarum* (Gibbs, 1980, SEM Figs. 51 & 54). The latter species also lacks the characteristic mushroom-shaped secondary seta found on the integument of many other mature *Lycaena* larvae. (See above.) Previous studies of adult *boldenarum* have shown that this unique butterfly may warrant distinct generic status (Sibatani, 1974). Further SEM examination of *boldenarum* and comparative studies of other lycaenine immatures may facilitate taxonomic decisions in this regard.

The pattern of proleg crochets, like other integument derivatives, also changes in later instars. Each proleg of the mature *epixanthe* larva has a large mesoseries of 60-70 crochets. These crochets are organized into two separate multiseries separated centrally (as in the first instar) by a fleshy spatulate lobe. Most significantly, a new element makes its appearance on the lateral aspect of the mature larval proleg. This element consists of a small horizontal row of five equal-sized crochets (uniordinal lateroseries) which are consistent in number from leg to leg. This lateroseries is found on other Nearctic (*hyllus, arota*) and Palearctic (*virgaurae, tityrus, helle*) species, but it proves not to be a unique lycaenine character as it is present in riodinids as well (Downey, pers. com.). However, this does not detract from its usefulness for comparative lycaenine studies. Gibbs (1980, SEM Fig. 45) has shown in New Zealand *Lycaena* that considerable interspecific variability exists in the number of crochets of the lateroseries.

Pupae of *epixanthe* are very small and obtect. They resemble the general lycaenid pupa in shape and display the same type of fine surface reticulations. Most of the pupae are green in color and heavily marked with black maculations making them quite inconspicuous when hidden among the cranberry leaves and sphagnum moss. Not all pupae are green and an unusual polymorphism exists for pupal color. Approximately five percent of the pupae are purple. Despite their atypical color, these pupae also blend imperceptibly into the speckled shadows of the cranberry vines and sphagnum on the bog floor. Origins of pupal polymorphism are not known, but they may occur widely in the lycaenine stock. Newcomb (1911) in his studies of *dorcas* reported small numbers of black puape and in a single instance a pupa colored "purple-madder".

The *epixanthe* pupal integument contains several unique cuticular derivatives (spiracle sculpturing, stridulatory organ, setae). Like those of the larva, lumina of pupal spiracles are decorated with coral-like sculpturing. This sculpturing is morphologically differentiated from larval spiracles, but a similar protective role is hypothesized for both. Virtually nothing is known about lycaenid pupal spiracles. A detailed study seems in order to determine if interspecific variability exists and if it can use taxonomically.

Like other lycaenids, *epixanthe* pupae contain a well-developed stridulatory organ located on the dorsum of intersegmental region A-5/A-6. The sound organ consists of a stridulatory file on A-6 with recurving teeth that grate against surface irregularities (grains and reticulations) of the stridulatory plate on A-5. This configuration is identical to the typical *Lycaena* sound organ found by Downey in eleven species of Palearctic and Nearctic *Lycaena* (Downey, 1966; Downey and Allyn, 1973).

The trumpet-shaped seta of *epixanthe* pupae is shared by many other *Lycaena* species. This seta was first described from the pupal case of *phlaeas* by T. A. Chapman (1905a) as a "trumpet-hair". Chapman subsequently recorded the same seta in other Palearctic *Lycaena* and speculated on its universal occurrence within the genus (Chapman, 1905b, 1906, 1907, 1913). The seta has since been recorded in *L. orus* and *clarki* (Clark and Dickson, 1971) of the Ethiopian realm; *L. salustius, rauparaha,* and *feredayi* (Gibbs, 1980) of the Indo-Australian realm; plus in Nearctic members *arota* (Comstock, 1928), *xanthoides* (Comstock and Dammers, 1935b), *editha* (Scott, 1979), *gorgon* (Comstock and Dammers, 1934), *hyllus* (Scudder, 1889), *heteronea* (Williams, 1910), *dorcas* (Newcomb, 1911), *helloides* (Coolidge, 1924; Comstock, 1929), *nivalis* (Newcomer, 1911), and *hermes* (Comstock and Dammers, 1935a). The seta has not been found on pupae of other lycaenid genera. Its ultrastructure was recently depicted by Downey and Allyn (1973, Figs. 60 & 61) and Gibbs (1980, Fig. 49). Downey and Allyn (1973) also noticed very small numbers of a second setal type (hydroid-type) on the sixth abdominal segment of some *Lycaena* species, but not others. This hydroid seta was present on *dispar* and *hyllus* pupae, but absent on *phlaeas* and *helloides*. The author did not find it on *epixanthe* pupae.

In conclusion, the author has attempted to elucidate *epixanthe*'s unique life history strategy for survival in the bog, while underlining the striking homogeneity of morphologic and development characters within the genus. Reproductive biology of adult butterflies is tightly coordinated with the hostplant flowering period, but success of the species is most likely linked to adaptive features of its ova and larval stages. The great majority of the butterfly's lifespan (85%) is spent in the egg stage where plastronic respiration is hypothesized to occur in order to circumvent the frequent hazard of submergence in flood water and rain water. Ova architecture consistent with plastron breathing is found within the highly sculptured topography of *epixanthe*'s chorionic coats. Many other overwintering Nearctic ova have comparable external sculpturing, suggesting that evolution of the *Lycaena* plastron may have been accomplished very early in the Nearctic line. Following the egg stage, larval ontogeny commences with first instars which are fixed with primitive features thought to reflect those of the lycaenine archetype. Comparative studies of *Lycaena* first instars are quite preliminary at this time, but early evidence points toward considerable homogeneity. It may be that morphologic conservatism has resulted in very little change in first instars during the course of evolution. After the first larval molt, a radical change takes place in larval anatomy and subsequent instars take on a substantially different appearance (hypermetamorphosis). As larval stages progress, integument derivatives of late *Lycaena* larvae still show striking comparative homogeneity, but patterns of larval coloration and behavior notably diverge in response to contrasting habitats and food preferences. It is through these latter adaptive modifications that *Lycaena* larvae will probably be found to differ most significantly. The same principle is also expressed in lycaenine pupae. The author cautions that many further ultrastructure studies of lycaenine immatures are needed to determine if certain characters show greater variability between congeners than others. Only then can the reliability and usefulness of immature characters be evaluated for taxonomic decisions.

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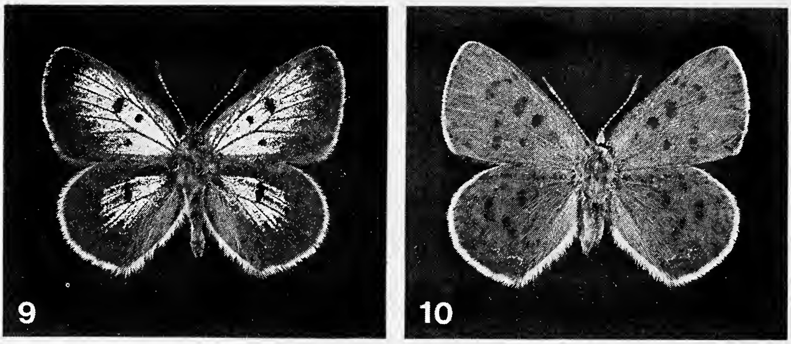


Figs. 9-10. Ultraviolet photography of adults. Forge Pond bog, Atlantic Co., N.J. **9.** Male. **10.** Female.

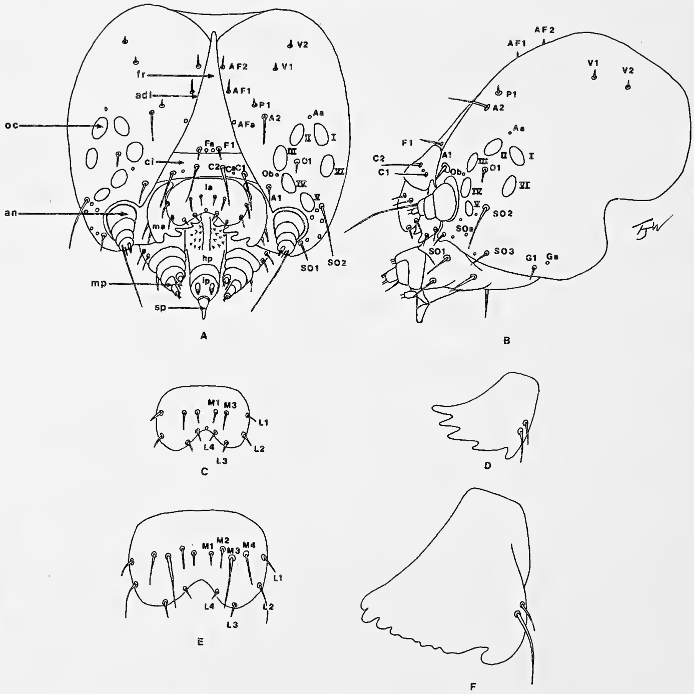


Fig. 11. Cranial chaetotaxy, first instar. A. Frontal view. B. Lateral view. C. Labrum, first instar. D. Mandible, first instar. E. Labrum, fourth instar. E. Mandible, fourth instar. Key to abbreviations: adl=adfrontal lateral suture, an=antenna, cl=clypeus, fr=frons, hp=hypopharynx, la=labrum, lp=labial palps, ma=mandible, mp=maxillary palp, oc=ocellus, sp=spinneret. Setal names and punctures explained in text.

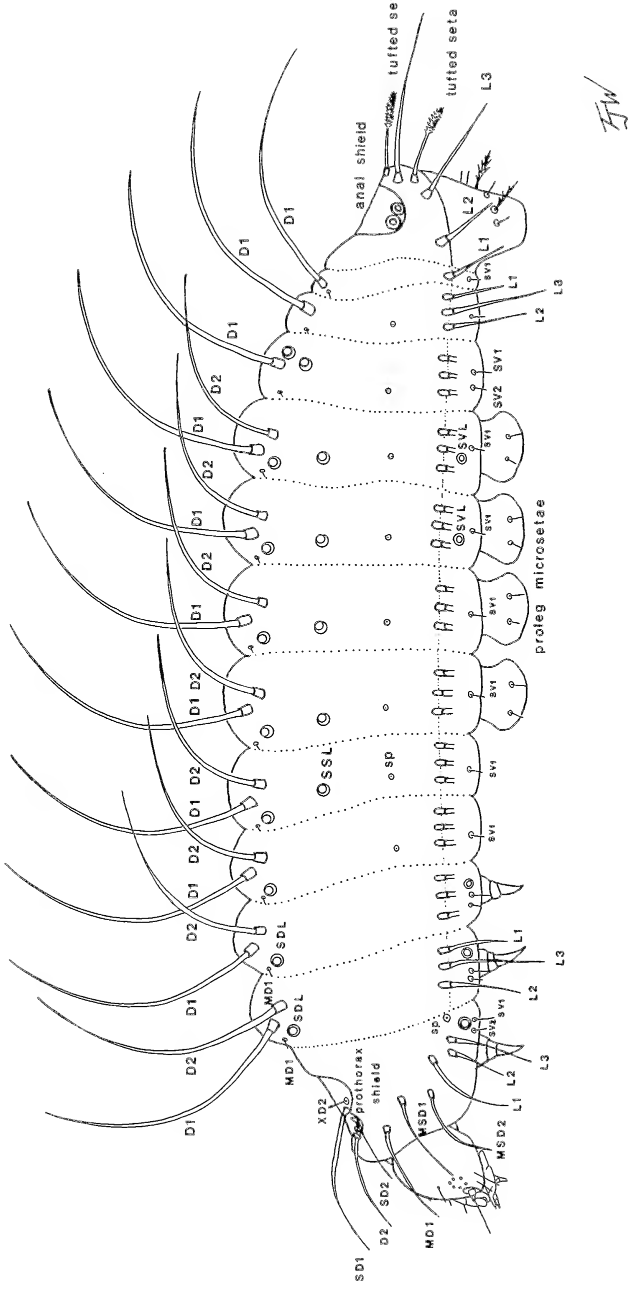


Fig. 12. Chaetotaxy of body, first instar. Left side labeled only.

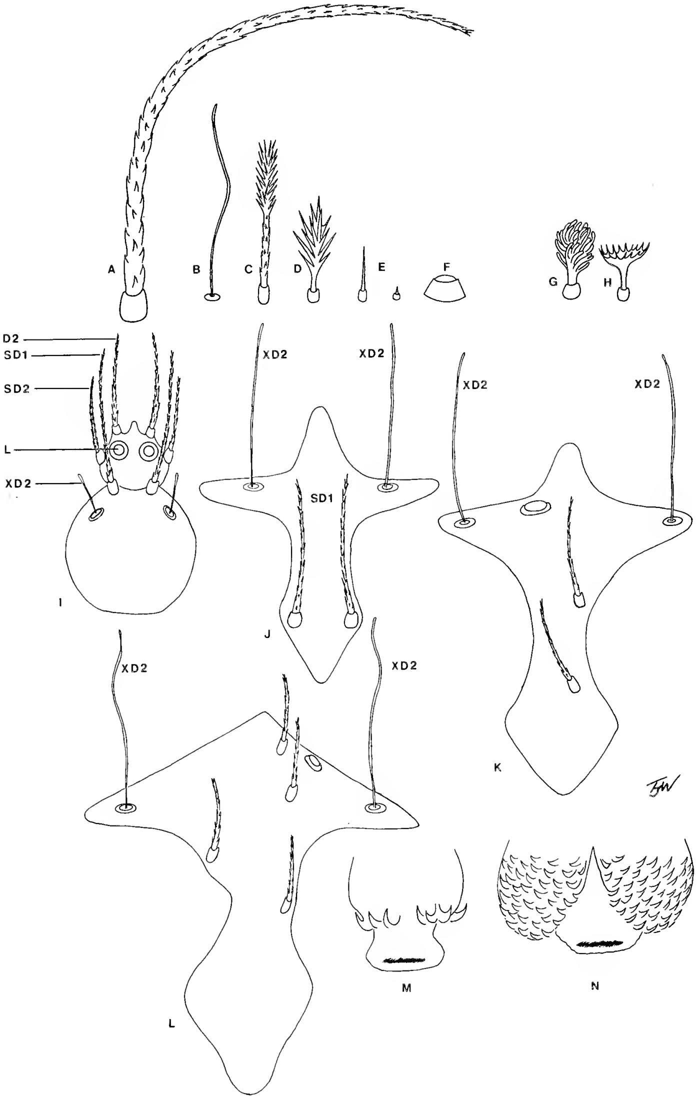
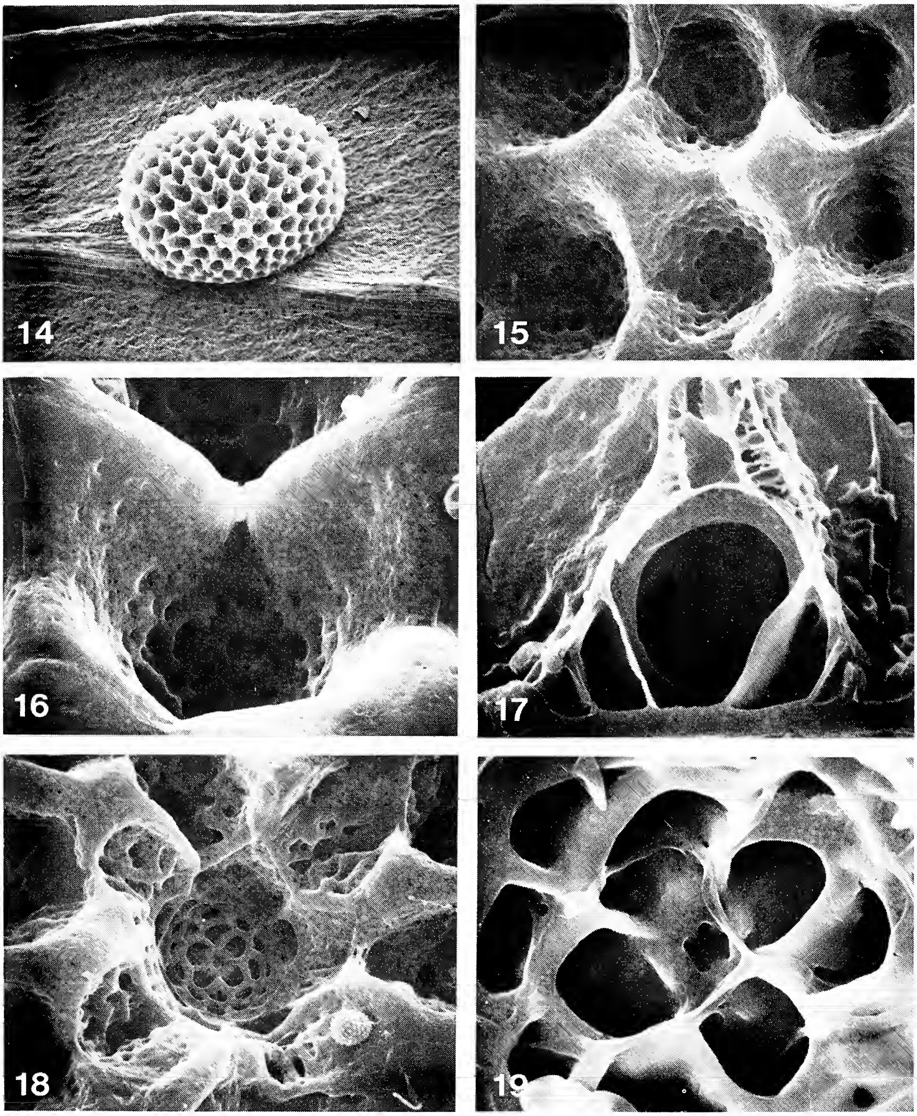
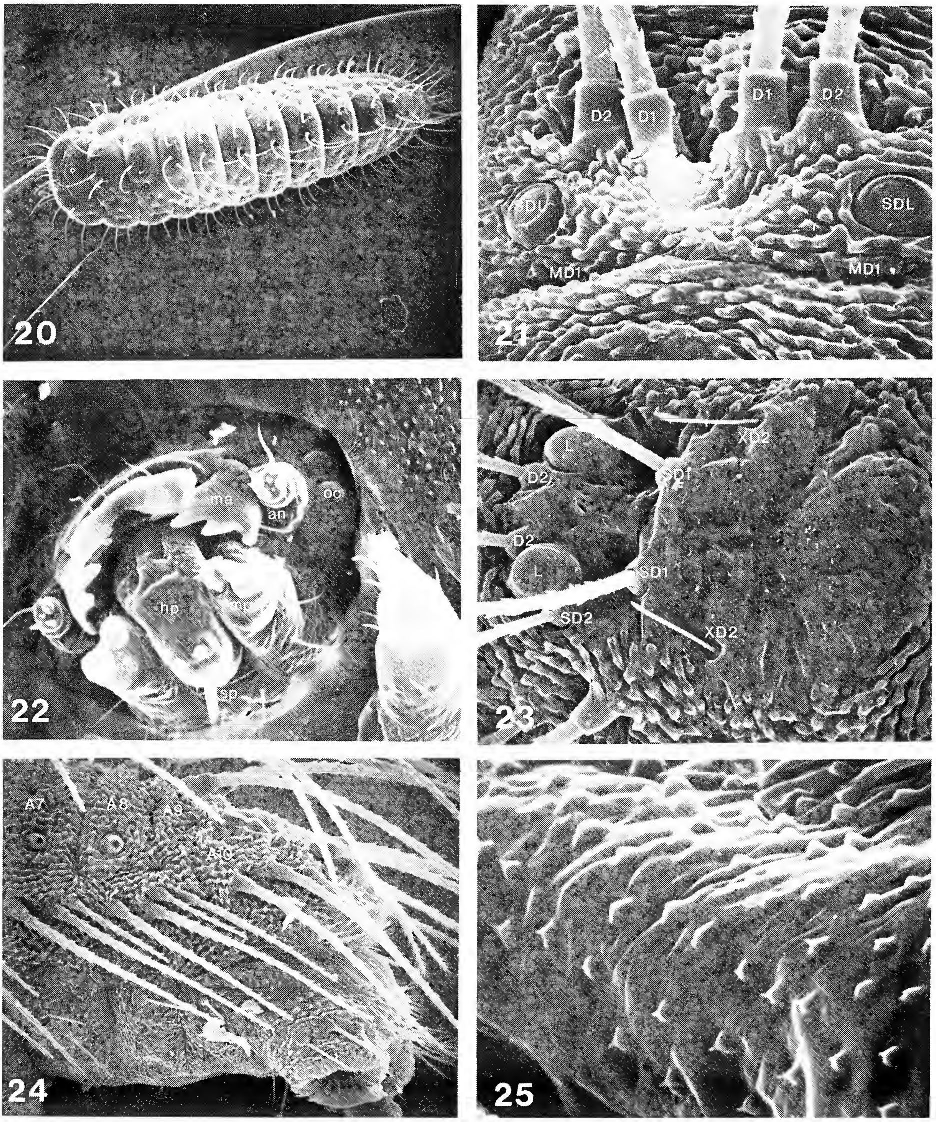


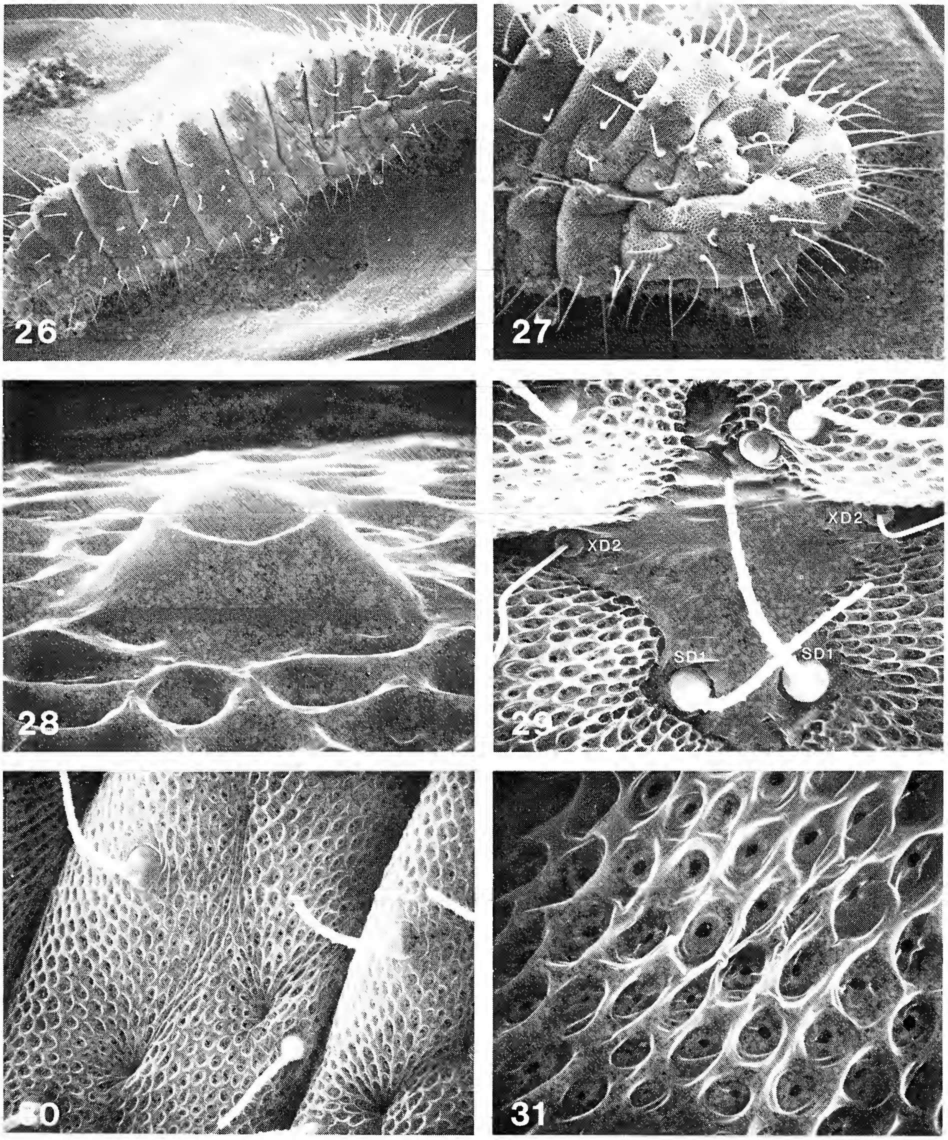
Fig. 13. A-E. Types of setae, first instar. A. Major spiculiferous seta. B. Filiform seta. C. Tufted seta. D. Thorny seta. E. Smooth non-spiculated setae, long tactile and short proprioceptive. F. Lenticle. G. Specialized secondary seta, fourth instar. H. Trumpet-hair seta, pupa. I-L. Prothoracic shield of first (I), second (J), third (K), and fourth (L) instar. M-N. Ventral prolegs, medial surface of first (M) and fourth (N) instar.



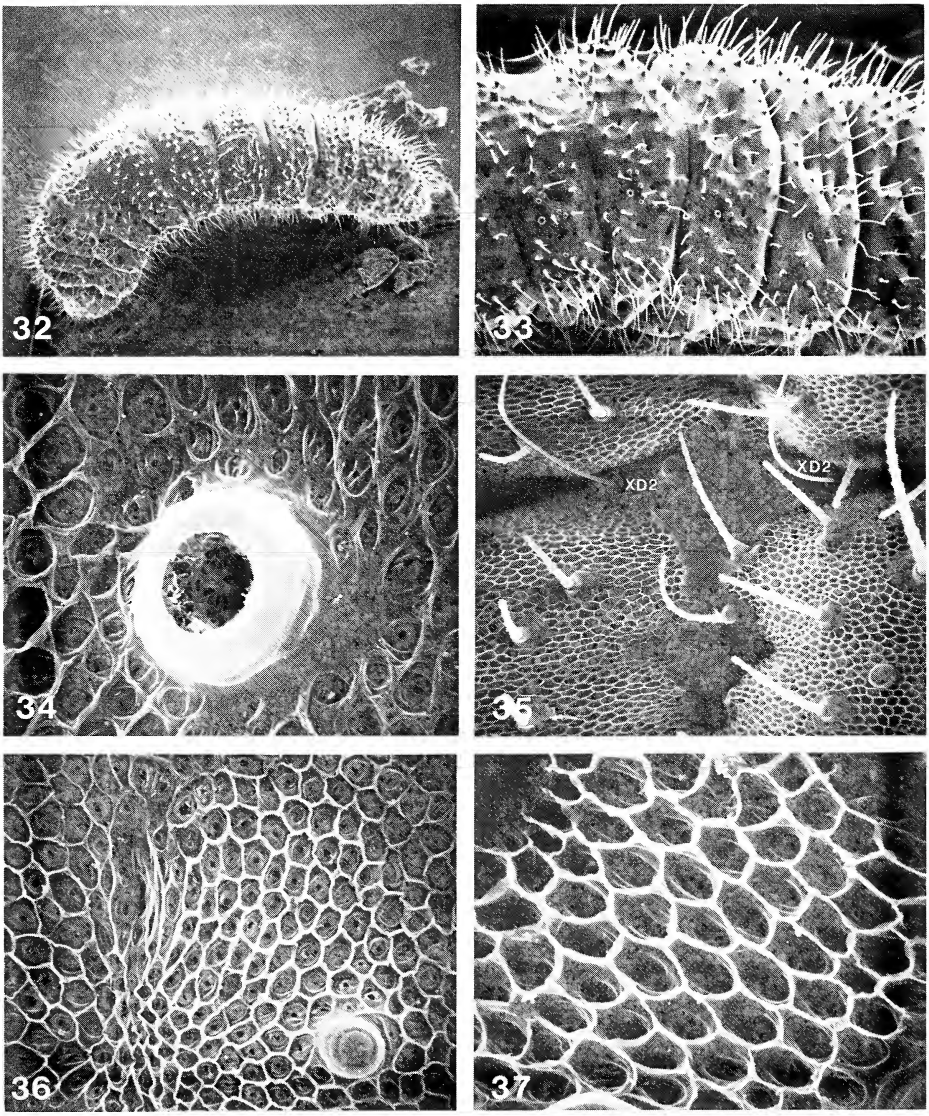
Figs. 14-19. SEM of ova. 14. Dome-shaped ovum with honeycombed chorion on undersurface of cranberry leaf. 80x. 15. Chorionic reticulum showing ridges and cells. 640x. 16. Chorionic cell. Note aeropyles at bottom of cell and thin membrane between ridges. 1250x. 17. Fractured chorion showing intrachorionic airspaces. 2100x. 18. Micropylar region. Pollen grain at lower right. 640x. 19. Micropyle and micropylar rosette. 2500x.



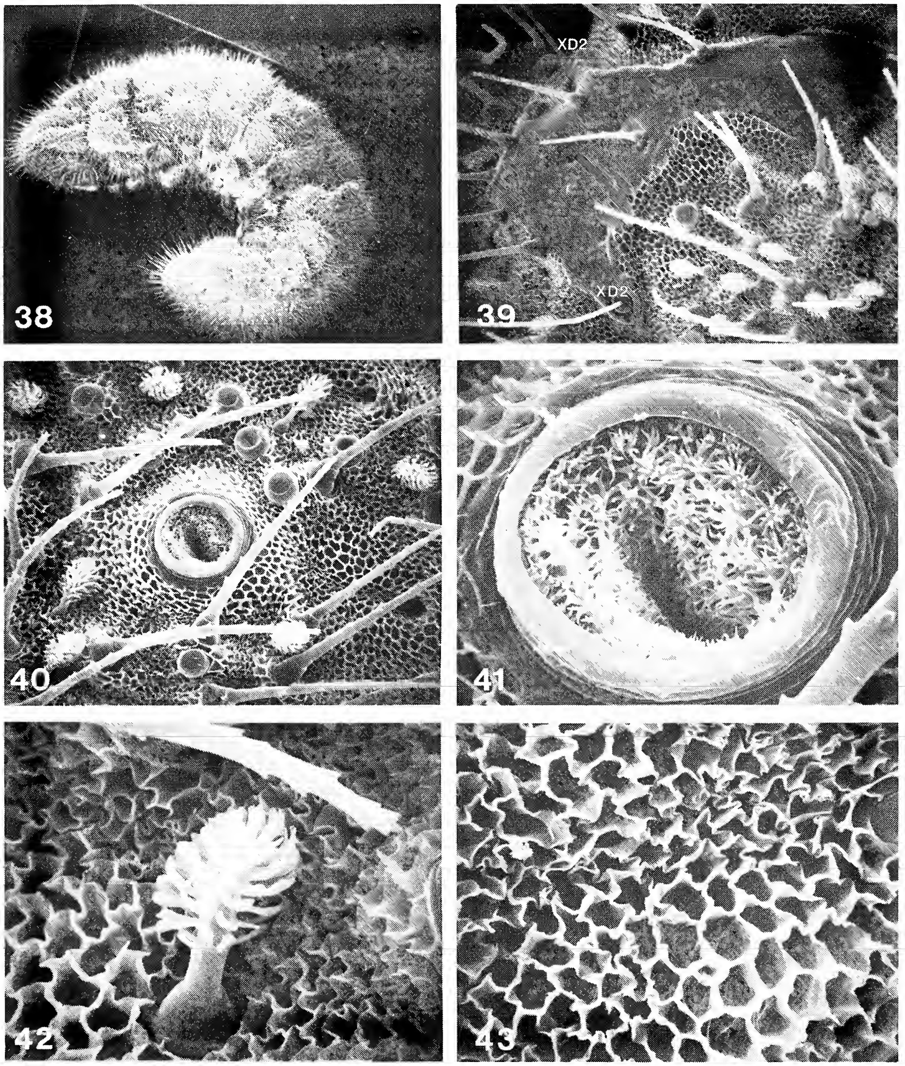
Figs. 20-25. SEM of first instar. 20. Whole larva, dorsal view. Anterior segments on left. Note setation and integument pits. 40x. 21. Mesothorax, dorsal view. Anterior margin of segment at bottom. 700x. 22. Larval head retracted into prothorax, frontal view. 410x. 23. Prothoracic shield. Anterior portion of shield at left. 640x. 24. Terminal segments of abdomen, lateral view. 320x. 25. Integument sculpturing. Note flat surface with microtubercles. 2180x.



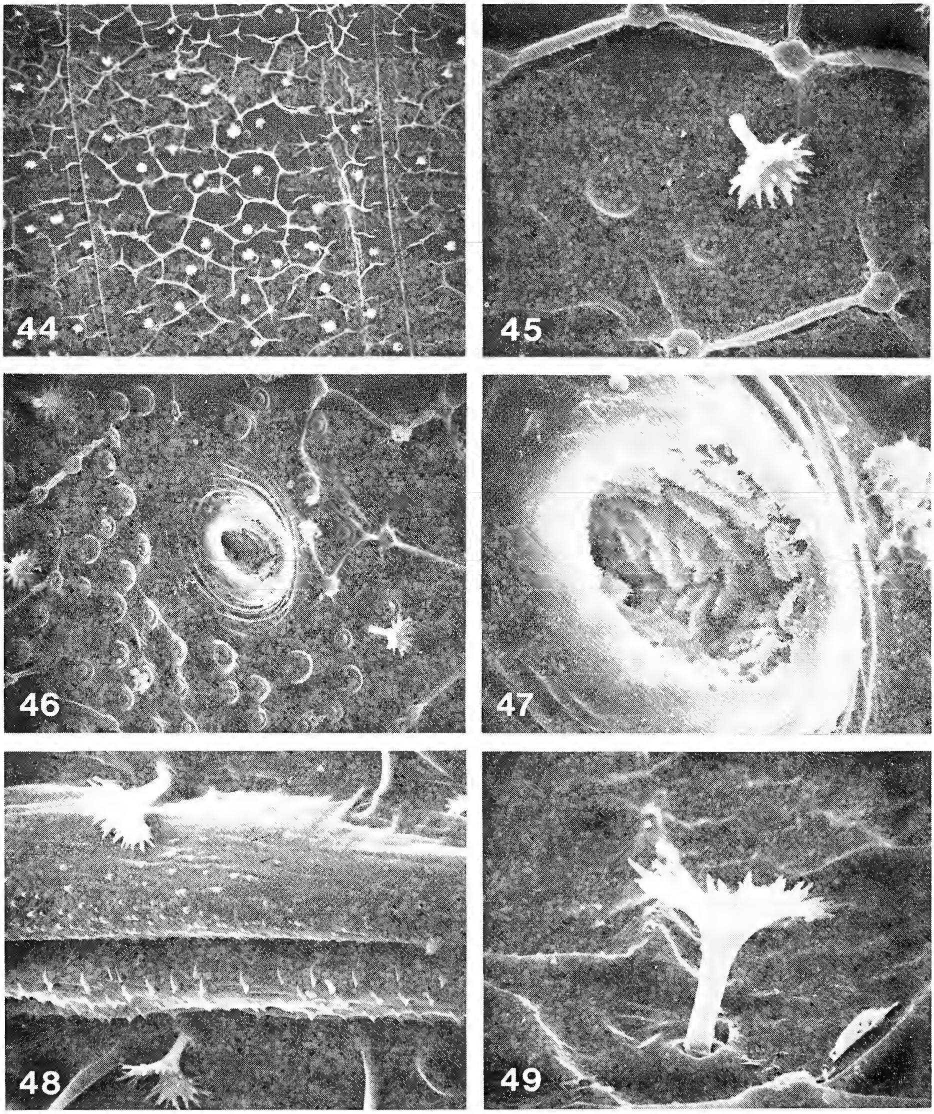
Figs. 26-31. SEM of second instar. 26. Whole larva, lateral view. Note holes eaten on undersurface of cranberry leaf. 40x. 27. Anterior end of larva. Prothorax with depressed shield. 80x. 28. Lenticle. 2500x. 29. Prothoracic shield. Anterior portion of shield at top. 450x. 30. Integument showing deep conical pits. 320x. 31. Integument sculpturing. Note depressed oval surface units. 1250x.



Figs. 32-37. SEM of third instar. 32. Whole larva, lateral view. Anterior segments on left. 20x. 33. Abdominal segments, lateral view. Note heavy secondary setation and integument pits. 46x. 34. Spiracle with internal sculpturing. 1250x. 35. Prothoracic shield. Anterior portion of shield at top. 240x. 36. Integument. Note pit in intersegmental groove. 640x. 37. Integument sculpturing. Note thin-walled partitions surrounding each surface unit. 1250x.



Figs. 38-43. SEM of fourth instar. 38. Whole larva, lateral view. Anterior segments at bottom right. Note extremely heavy secondary setation. 15x. 39. Prothoracic shield. Anterior portion of shield at left. 240x. 40. Integument showing spiracle surrounded by lenticles, major secondary setae, and specialized secondary setae. 320x. 41. Spiracle close-up showing internal sculpturing. 1250x. 42. Specialized secondary seta, "mushroom"-like. 1250x. 43. Integument sculpturing. Note tall thin-walled partitions surrounding each surface unit. 1250x.



Figs. 44-49. SEM of pupa. 44. Pupal integument showing fine elevated ribs. 80x. 45. Integument close-up showing ribs, sensory verrucae, and seta. 640x. 46. Spiracle densely surrounded by sensory verrucae. 320x. 47. Spiracle close-up showing internal sculpturing. 1250x. 48. Stridulatory organ on intersegment A-5/A-6. Stridulatory plate at top (A-5) and file at bottom (A-6). 640x. 49. Pupal "trumpet-hair" seta. 1250x.

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**Manuscript Format: Two** copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

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## IN THIS ISSUE

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COVER ILLUSTRATION: Scanning electron micrograph of first instar larva, dorsal view, *Lycaena epixanthe*, see Wright, page 47.

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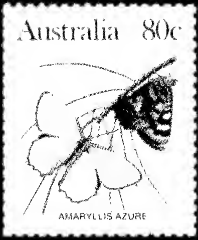

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# *Speyeria atlantis* Phenotypes in the Southern Rocky Mountains (Lepidoptera: Nymphalidae: Argynninae)[1]

Clifford D. Ferris[2]

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**Abstract.** Phenotypes of *Speyeria atlantis* found along the Front Range of the Rocky Mountains from southeastern Wyoming to north-central New Mexico are described and discussed.

## Introduction

The first publication to detail the distribution of *Speyeria atlantis* (W. H. Edwards) along the Colorado Front Range was by Brown, Eff & Rotger (1955, 1957). Subsequently, A. H. Moeck (1957, 1975) published a monograph on the geographic variability of *Speyeria* in North America. He included a general discussion of *S. atlantis* in the Rocky Mountain region. Since Moeck's monograph appeared, extensive collecting in Wyoming, Colorado and New Mexico by numerous individuals has greatly extended our knowledge of the distribution of this insect. A brief treatment covering Wyoming was published by Ferris (1971), and a summary of contemporary information can be found in Ferris & Brown (1981). A very much expanded discussion from this latter work is now presented.

## Taxonomic Background

In the region encompassed by this paper, *Speyeria atlantis* occurs in appropriate habitats from 5900′ (1800 m) to timberline at roughly 12,000′ (3660 m) in southern Colorado. In southern Wyoming, timberline begins at about 10,800′ (3295 m). *Viola* species serve as the larval hosts, and *atlantis* may be found in riparian canyons, mountain meadows, and wooded areas in association with these plants. Adults are particularly attracted to nectar sources belonging to the mint family, especially wild bergamont (*Monarda* sp.). These butterflies behave rather differently in different geographic localities, apparently indicative of adaptation to local ecological conditions involving their larval hosts.

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[1] Published with the approval of the Director, Wyoming Agricultrual Experiment Station as Journal Article No. JA 1189.

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Four distinct forms of *S. atlantis* occur along the Front Range; three of which have been given subspecific recognition. In addition, various clines or intergrades can be identified.

The first subspecies to be named was *hesperis* (W. H. Edwards), 1864. This was followed by *electa* (W. H. Edwards), 1878, and finally *nikias* (Ehrmann), 1917. In 1892, W. H. Edwards also named *cornelia*, now considered by most specialists to be a synonym of *electa*. As is the case with many butterflies named during the 1800s, the type localities of these *atlantis* subspecies were somewhat vague.

In 1947, dos Passos & Grey published a paper in which they attempted to fix the type localities of all of the North American *Speyeria*, and to identify holotypes, or designate lectotypes or neotypes as the case required. In 1965 as part of his continuing series of monographs on the W. H. Edwards butterfly names, Brown re-examined and revised some of the conclusions reached by dos Passos & Grey. The current designation of type localities as it appears in Miller & Brown (1981) is as follows: *hesperis*, Turkey Creek Junction, Jefferson Co., Colorado (fixed by dos Passos & Grey, confirmed by Brown); *electa*, Turkey Creek Junction, Jefferson Co., Colorado (fixed by dos Passos & Grey as Rocky Mountain National Park, Colorado, and revised by Brown); *nikias*, Jemez Springs, Sandoval Co., New Mexico; *cornelia*, Ouray, Ouray Co., Colorado (fixed by dos Passos & Grey, confirmed by Brown).

The basis upon which Brown changed the type locality for *electa* rests upon the fact that T. L. Mead, who collected the type specimen in 1871, did not collect in the region now occupied by Rocky Mountain National Park. This insect, however, does occur in the Park.

From my field experience, I doubt that the type of *nikias* came from Jemez Springs, *per se*. More likely, it was taken at higher elevation a few miles to the north in the Jemez Mts., where these butterflies abound at the edges of forest clearings.

The fixation of type localities by Brown has generated a problem in that two subspecies now have the same type locality. This raises the following question: If *atlantis*, in fact, is a valid biological species, then how can two distinct subspecies occur at the same locality? Given our present knowledge several answers may apply. An obvious one is simply that one of the type localities is incorrect. Both *hesperis* and *electa* phenotypes, however, do occur sympatrically and synchronously in many areas. Thus the types that represent both taxa may indeed have been collected in the same locality. Another answer is that *hesperis* and *electa* are sibling species in the "*atlantis* complex". Rearing studies, which have yet to be carried out (see below), should prove or disprove this theory. A third answer is that *atlantis* along the Front Range is polymorphic. My own field studies indicate that this is an attractive possibility substantiated in part by data subsequently presented.

The obvious soution to the questions and answers posed above would be provided by controlled rearing studies in the laboratory. This solution is not so simple as it appears. Techniques for rearing *Speyeria* have been published (Mattoon, et al., 1971), but persons attempting to rear *S. atlantis* have experienced various difficulties. G. D. Willis (pers. comm.) has experienced little difficulty in rearing the larvae to adults once ova were obtained. He has found *atlantis* females from eastern North America to be very reluctant to oviposit in captivity. Gravid females that I sent to him of the Wyoming *hesperis* and *electa* phenotypes refused to oviposit.

Sterling O. Mattoon (*in litt.*) has reared Rocky Mountain *atlantis*, but ova and larvae were not segregated as to female parent. Thus clear data are not available. It is his impression from controlled rearing of ova from other populations that adult series are polymorphic to some degree. He cites as the probable cause the differences between environmental conditions in the laboratory and in nature, and multiple matings of the females with different males.

On the other hand, L. P. Grey (*in litt.*) has stated that the reared series of *Speyeria* that he has examined tend to follow the phenotype of the female parent. Thus we have equivocal results from the rearing attempts that have been conducted to date.

What is needed is a series of laboratory experiments in which virgin females are hand-paired with males, so that the phenotypes of both parents are clearly known. Wild-caught pairs *in copulo* will not suffice, since the number of matings that the females have experienced cannot be determined, except by dissection, and this procedure would not identify male phenotype. In some nymphalids, the ova are fertilized only by the last mating and wild-caught pairs would suffice; however it is not known if this is the case with *Speyeria*. Mattoon stated that he has had no success in attempts to hand-pair *Speyeria*. Thus for the present, we must rely upon field data.

## Discussion of Principal Phenotypes

The main character by which the *atlantis* phenotypes in the Front Range are separated lies in the discal area of the ventral hind wings. Both discal color and the nature of the pale spots are used. In *hesperis*, the disc is medium brown, and the spots are cream-colored and opaque. The disc in *electa* is dark brown (almost purplish-brown in some fresh specimens) beset with bright silver spots. The disc in *nikias* is red-brown or brick-red, and the spots are silvered. Of the Front Range phenotypes, *electa* is the closest to the "parent" or Appalachian population. Nominate *atlantis* occurs in the northeastern United States and in southeastern Canada in Canadian zone or boreal environments. A relict population exists in the Black Hills refugium in western South Dakota and northeastern Wyoming. A fourth phenotype, to be discussed subsequently, occurs in Las Animas

Co., Colorado and adjacent Colfax Co., New Mexico.

In most cases, *hesperis* is a low-elevation insect associated with riparian canyons, although it may be taken throughout the Transition zone and into the lower Canadian zone. It is often out in the open nectaring at thistles in meadows, and at various members of the mint family along streams. I have taken specimens at 9500′ (2900 m) in the Snowy Range, Albany Co., Wyoming, but *hesperis* is usually encountered at elevations from 5900-8500′ (1800-2600 m). Figures 1-2 illustrate *hesperis*.

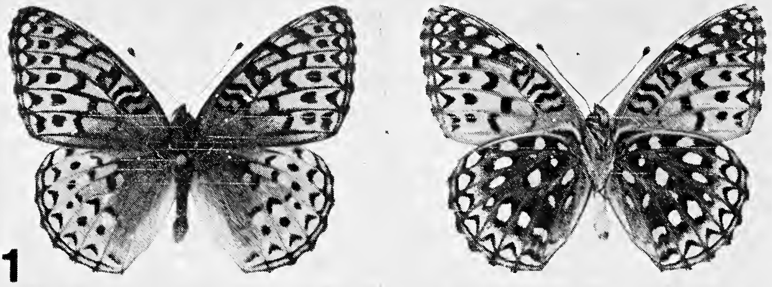

Fig. 1. *S. atlantis hesperis* male, D (left), V (right). Boulder Can., Boulder Co., CO, 21 vii 65.

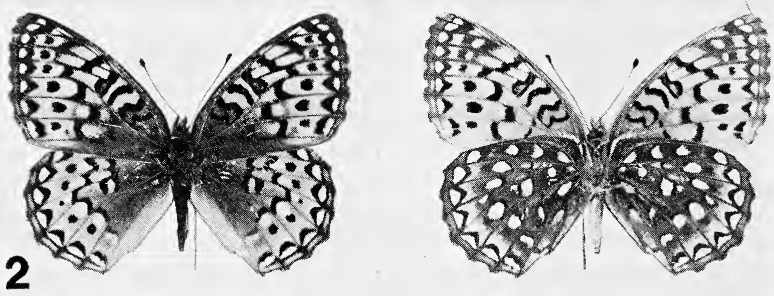

Fig. 2. *S. atlantis hesperis* female, D (left), V (right). Flagstaff Mt., Boulder Co., CO, 7 viii 68.

I normally ssociate the *electa* phenotypes with forest roads and the edges of forest clearings at elevations above 8000′ (2440 m). In southern Wyoming, it occurs sympatrically and synchronously with *hesperis* at approximately 8200′ (2500 m) in the Sherman Range of the Laramie Mts., the Snowy Range, and the east slope of the Sierra Madre Mts. The vegetative association is aspen-conifer. Figures 3-4 illustrate *electa*.

The *nikias* phenotype is generally distributed along the Western Slope in Colorado, rather than in the Front Range. On the west slope of the Sierra Madre Mts., Carbon Co., Wyoming, specimens referable to *nikias* can be taken along with *hesperis* and *electa* forms. The vegetative association is oak-aspen-conifer. South of this region on a line through Rabbit Ears Pass,

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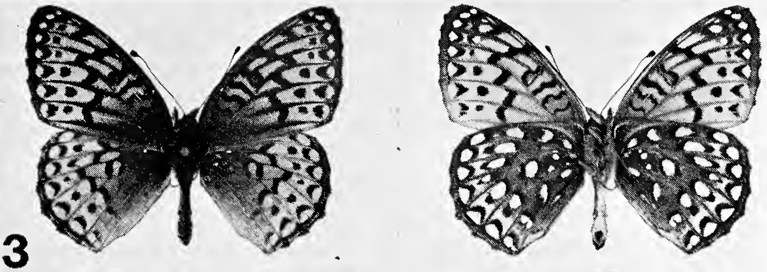

Fig. 3. *S. atlantis electa* male, D (left), V (right). Pole Mt., Medicine Bow Nat. For., Albany Co., WY, 18 vii 71.

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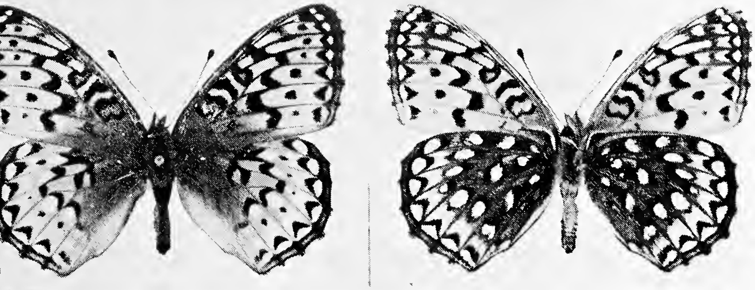


Fig. 4. *S. atlantis electa* female, D (left), V (right). Foxpark, Albany Co., WY, 1 viii 69.

Routt Co., Colorado and along the Western Slope, *nikias* is the predominant form, although the *electa* phenotype is frequently encountered. The *nikias* phenotype usually flies in aspen-conifer regions, and I have seen it at timberline at the base of Mt. Uncompahgre in Hinsdale Co., Colorado. This butterfly occurs at the edges of forest clearings in aspen-conifer habitat in Rio Arriba, Santa Fe and northern Sandoval Cos., New Mexico. The typical altitude range in New Mexico is 7900-8500′ (2400-2600 m). Figures 5-6 illustrate *nikias* from the Jemez Mts.

The most distinctive of the four phenotypes occurs in the high mesa regions to the northeast of Raton, New Mexico. The vegetative association where I have taken this butterfly is oak-conifer. The adults normally remain well inside the forested areas, rather than out in the open meadows, and fly in the sunshine and shadow of the forest glades. Both *Rudbekia* sp. and thistles are favored nectar sources.

This phenotype is the palest colored *atlantis* that I have encountered. In facies, flight pattern, and general habits, it is very similar to the subspecies *greyi* Moeck from Elko Co., Nevada, although somewhat larger and paler yet than *greyi*. Adults of both sexes tend to flutter close to the ground through the vegetation, and frequently perch on the ground, a characteristic also of *greyi*. When startled, however, they are determined fliers as in other subspecies of *atlantis*. Figures 7-8 depict this phenotype.

Ferris (in Ferris & Brown, 1981, p. 311) stated regarding this pale phenotype: "The variation within a given colony is too great to consider assigning subspecific status to this entity". Until the problems of speciation and polymorphism in *atlantis* are resolved, it seems unwise to erect additional subspecific taxa in this complex. While this paper was undergoing initial review, however, Scott (1981) proposed the name *ratonensis* for the pale phenotype. It is not clear that this publication meets all of the requirements of the Code of the I.C.Z.N. The designated holotype from Raton Mesa, Colfax Co., New Mexico is apparently deposited in the collection of the Los Angeles County Museum of Natural History, Los Angeles, California.

Various intergrade or clinal forms among the four principal phenotypes are regularly encountered. These will be discussed in the next section which treats the distribution of the *atlantis* complex in the central Rocky Mountain region.

## Distribution of Phenotypes

Figure 9 shows the distribution of *S. atlantis* phenotypes in the geographic region of interest. Two other subspecies occur in New Mexico:

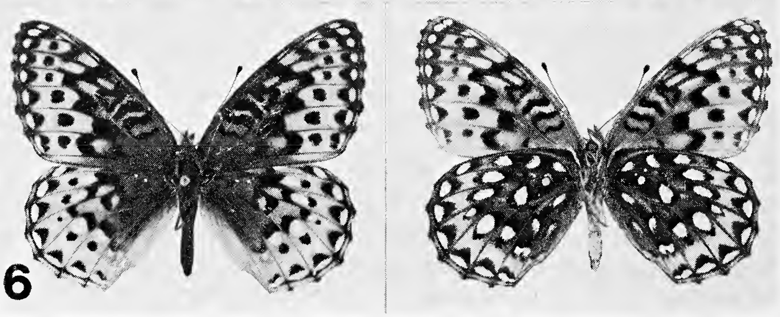
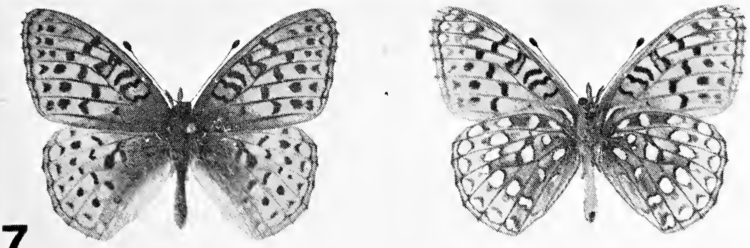


Fig. 5. *S. atlantis nikias* male, D (left), V (right). Clear Creek C.G., Santa Fe Nat. For., Rio Arriba Co., NM, 10 vii 79.

Fig. 6. *S. atlantis nikias* female, D (left), V (right). Clear Creek C. G., Santa Fe Nat. For., Rio Arriba Co., NM, 10 vii 79.



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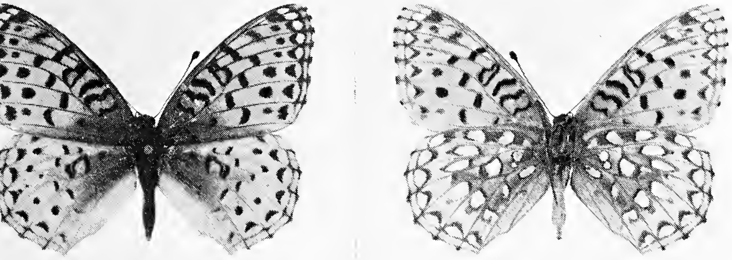

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Fig. 7. *S. atlantis* pale phenotype male, D (left), V (right). Upper Sugarite Canyon, Las Animas Co., CO, 4-5 viii 81.

Fig. 8. *S. atlantis* pale phenotype female, D (left), V (right). Upper Sugarite Canyon, Las Animas Co., CO, 4-5 viii 81.

*dorothea* Moeck, just to the south of where the map ends, and *nausicaa* (W. H. Edwards) in the southwestern part of the state. These subspecies do not interact to any extent with the butterflies under discussion, and will not be further mentioned. Other non-interacting subspecies occur to the north and west of the region illustrated.

From the map, it is clear that *hesperis* generally occupies the Colorado Front Range, and *nikias* the Western Slope. Above 8000′ (2440 m), *electa* may be found on either side of the Continental Divide in both Colorado and Wyomng. In New Mexico, west of the southern extension of the Sangre de Cristo Mts., and into the Jemez Mts. in Rio Arriba, Santa Fe and northern Sandoval Cos., we find *nikias*. The pale phenotype *ratonensis* occurs in basically undiluted form in extreme northeastern Colfax Co., New Mexico and into the contiguous portion of southern Las Animas Co., Colorado.

Over most of Taos Co. and extreme western Colfax Co., New Mexico, the predomnant form is an intermediate between *nikias* and *electa*. The spots on the disc are silvered, and the ground color is generally dark, occasionally with some basal olivaceous scaling (Cabresto Canyon, Taos Co.). On an individual basis, many specimens are referable to *nikias*, but when taken in series intermediate forms are apparent.

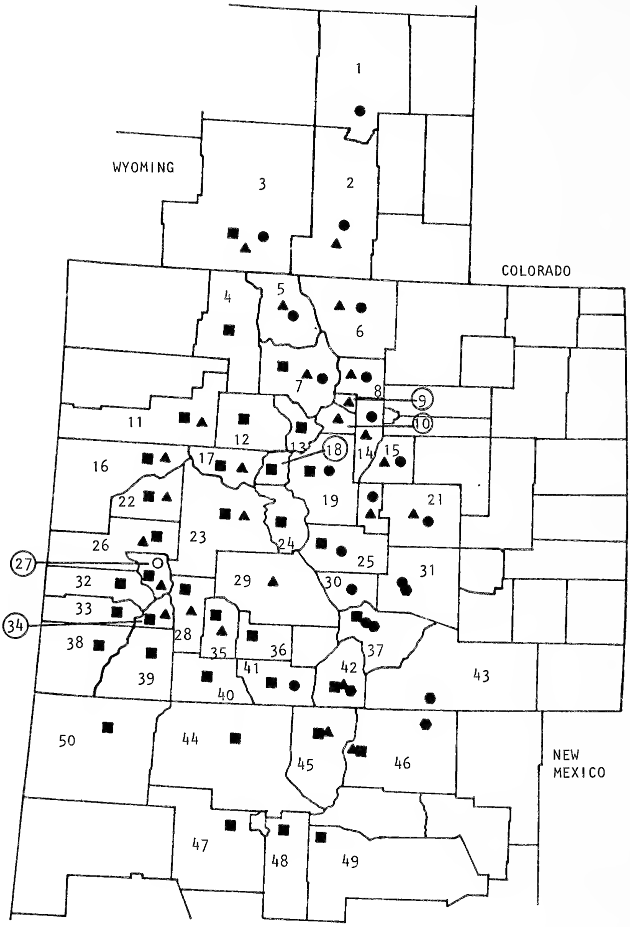
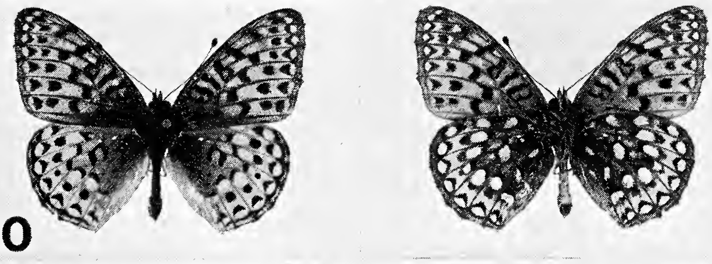


Fig. 9. Distribution of *S. atlantis* in southern Wyoming, Colorado and northern New Mexico. Solid dots = *hesperis*; triangles = *electa*; squares = *nikias*; hexagons = pale phenotype. Conjoined symbols emphasize clines. County names corresponding to map numbers: 1. Converse, 2. Albany, 3. Carbon, 4. Routt, 5. Jackson, 6. Larimer, 7. Grand, 8. Boulder, 9. Gilpin, 10. Clear Creek, 11. Garfield, 12. Eagle, 13. Summit, 14. Jefferson, 15. Douglas, 16. Mesa, 17. Pitkin, 18. Lake, 19. Park, 20. Teller, 21. El Paso, 22. Delta, 23. Gunnison, 24. Chaffe, 25. Fremont, 26. Montrose, 27. Ouray, 28. Hinsdale, 29. Saguache, 30. Custer, 31. Pueblo, 32. San Miguel, 33. Dolores, 34. San Juan, 35. Mineral, 36. Rio Grande, 37. Huerfano, 38. Montezuma, 39. La Plata, 40. Archuleta, 41. Conejos, 42. Costilla, 43. Las Animas, 44. Rio Arriba, 45. Taos, 46. Colfax, 47. Sandoval, 48. Santa Fe, 49. San Miguel, 50. San Juan. Open symbol = dubious record.



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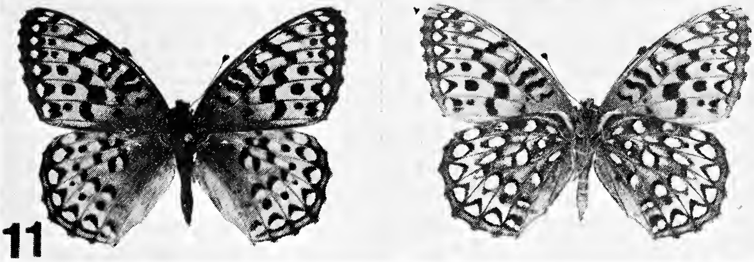

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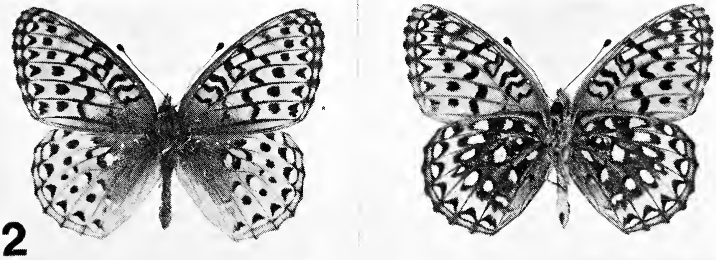
Fig. 10. *S. atlantis* male, D (left), V (right). La Veta Pass, Huerfano/Costilla Co., CO, 3 viii 81.

Fig. 11. *S. atlantis* female, D (left), V (right). La Veta Pass, Huerfano/Costilla Co., CO, 3 viii 81.



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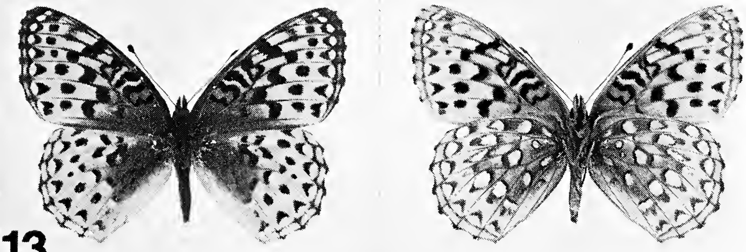

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Fig. 12. *S. atlantis* intermediate disc male, D (left), V (right). Cuchara Canyon, Huerfano Co., CO, 3-4 viii 81.

Fig. 13. *S. atlantis* pale disc female, D (left), V (right). Cuchara Canyon, Huerfano Co., CO., 3-4 viii 81.

In some respects, *nikias* is an unfortunate taxon. Material from the Jemez Springs region exhibits considerable variability, and not the stability of phenotype normally associated with a subspecific entity. Thus we must apply the name *nikias* in a broad sense and not in a strict sense.

Moving northward into Costilla Co., Colorado, both *nikias* and *electa* phenotypes have been recorded. In the vicinity of La Veta Pass in northeastern Costilla Co. and roughly central Huerfano Co., a cline exists, examples of which are shown in Figures 10-11. These butterflies generally have silver spots, but some individuals, females especially, may have partially silvered or opaque spots. Discal color is generally medium brown as in *hesperis*, darkening in some specimens to that of *electa*. An occasional pale specimen may be taken. In this region, the butterflies appear to prefer heavily wooded areas, but they may occasionally be taken in the open along streams and at the edges of clearings.

A curious blending of phenotypes occurs in southwestern Huerfano Co. from Cuchara Canyon (9100′, 2775 m) eastward to Cordova Pass (formerly called Apishapa Pass, 11,000′, 3350 m). Both silvered and unsilvered forms occur, and the discal color ranges from as pale as *ratonensis* to as dark as typical *nikias*. Typical specimens are illustrated in Figures 12-13. In this region, the butterflies are sometimes taken in open meadows near streams, but they seem to prefer heavily wooded areas. Thistles are a favored nectar source. Figure 14 shows a dark-disc specimen from Cuchara Canyon.

Dark-disc specimens are very rare in the *ratonensis* population. Based upon my field work, they represent about two percent of the total. In these cases, the discal color approximates that of a pale *hesperis*. Figure 15 shows a dark-disc specimen from Sugarite Canyon near Raton, New Mexico.

In the Rockies, occasionally unsilvered specimens are recorded from normally silver-spotted populations of *atlantis*. This perhaps accounts for records of *hesperis* from the Western Slope in Ouray Co., Colorado. along the Front Range, specimens with partially silvered spots occur frequently, especially in the females. Material from extreme western Colorado occasionally exhibits some influence from the red-disc paler forms found in southern Utah and northern Arizona.

## Conclusions

Field data at hand produce a mixed picture of the *Speyeria atlantis* complex in the geographic region under discussion. Results from rearing attempts to date are inconclusive. In the northern portion of the region (Sierra Madre Mts., Carbon Co., Wyoming), field-collected specimens are indicative of a cline that runs from *hesperis* through *electa* to *nikias*. Two apparent parallel clines exist in the southern portion of the region. In Taos Co., New Mexico, the *nikias* and *electa* phenotypes form the two ends of a cline. In southeastern Colorado, the cline runs from the pale *ratonensis* phenotype through *hesperis* and *electa* into *nikias*.

Preliminary enzyme electrophoresis studies were conducted by Angela F. Tebaldi, a graduate student at the University of Wyoming (1982). The enzymes extracted from ground preparations of adult *Speyeria atlantis* specimens and subjected to electrophoresis separation were: malic dehydrogenase, malic enzyme, glutamate dehydrogenase, isocitrate dehydrogenase, $\alpha$-glycerophosphate dehydrogenase, glutamate oxalotransaminase. The results of her studies indicate substantial heterozygosity in the Cuchara Canyon and Sierra Madre Mts. populations. This supports the cline theory. These data are presented in the Appendix. Other populations have not been studied by electrophoresis. On the Western Slope, however, field observations of pairs *in copulo* indicate the absence of mixed phenotype pairs (*fide* Scott L. Ellis). This observation supports the sibling species theory, and that there is some sort of isolating mechanism between *nikias* and *electa*.

Along the Front Range, there are some localities where *hesperis* and *electa* fly together, but intermediates are not recorded, again supporting the sibling species theory.

Based upon the available data, one may draw the following conclusions: Within the central massif in Colorado, there is an unknown isolating mechanism that causes *electa* and *hesperis*, and *electa* and *nikias* to behave as sibling species. At the north and south poles of the region under discussion, this isolating mechanism has broken down and we find heterozygous and polymorphic populations.

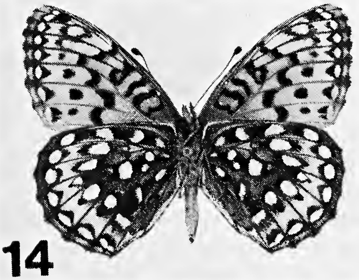

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Fig. 14. *S. atlantis* dark disc female, V. Cuchara Canyon, Huerfano Co., Co., 3-4 viii 81.

Fig. 15. *S. atlantis* dark disc female, V. Upper Sugarite Canyon, Las Animas Co., CO., 4-5 viii 81.

The *electa* phenotype apparently represents the parent *atlantis* stock. It prefers a boreal habitat, as is the case with nominate *atlantis*, other northern subspecies, and the Black Hills segregate. During the last ice age when boreal forest occupied what is now the Great Plains, there was probably a single dark *atlantis* phenotype. Following the retreat of the glaciers and the resultant warming and drying out of the Plains, this entity found refugia in the Rocky Mts., the Black Hills, and the Canadian border states.

The pale phenotype *ratonensis* found in the Raton and Johnson Mesa area perhaps represents an offshoot of a pale species that occupied a more savanna-like environment in the Southwest during the last ice age. There are parallel forms in southern Utah and Nevada.

The origin of the *hesperis* phenotype is unclear. There are various races of opaque-spotted *atlantis* throughout the western United States. In the Black Hills, one such form (*lurana* dos Passos & Grey) is sympatric and synchronic with the dark-disc silvered form. Intermediates do occur, but they are not at all common. Both the silvered and unsilvered forms occur in about equal numbers at some localities. One can iterpret the field data from the Black Hills as supporting the sibling species theory, rather than polymorphism in a single species produced, perhaps, by environm,ental factors.

Only carefully controlled rearing experiments in the laboratory, as noted previously, will resolve the questions that surround the *Speyeria atlantis* complex.

It should be noted that the division made by Howe (1975) of the *atlantis* complex into *atlantis* and *electa* is not correct based upon current knowledge. The *electa* phenotype belongs with nominate *atlantis*, while *hesperis* perhaps represents a sibling species.

*Acknowledgments:* I would like to thank the following individuals who provided field notes and other data used during this study: K. Bagdonas, Laramie, WY; J. D. Eff, Boulder, CO; S. L. Ellis, Ft. Collins, CO: L. P. Grey, Lincoln, ME: M. L. Howard, Pueblo, CO; S. O. Mattoon, Chico, CA; O. D. Spencer, Lincoln, NE: R. E. Sanford, Denver, CO: G. D. Willis., Holliston, MA. Two anonymous reviewers commented upon the manuscript, one of whom suggested inclusion of the Appendix.

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## Appendix

The data presented in Table 1 are excerpted from the work of Tebaldi (1982), p. 21). The *Speyeria atlantis* populations for which data are presented occur geographically as follows: (Battle Creek) Vic. Battle Creek Campground, Sierra Madre Range, ca. 7400′ (2257 m), Albany Co., Wyoming. (Cuchara Canyon) Vic. Cuchara Canyon Campground, Spanish Peaks, ca. 9300′ (2836 m), Huerfano Co., Colorado. The abbreviations used in the table are as follows: *MDL* = Malic dehydrogenase. *ME* = Malic enzyme. *GDH* = Glutamate dehydrogenase. *IDH* = Isocitrate dehydrogenase. *αGPdH* = α-glycerophosphate dehydrogenase. *GOT* = Glutamate oxalotransaminase. The subscripts designate different fractions of the related enzyme. *n* = the number of genomes sampled. *het* = the frequency of heterozygotes. *ca* = common allele. *N* = null allele. *sc* = slow common allele. *fc* = fast common allele. *s* = slow allele relative to the common allele *ca*. *f* = fast allele relative to the common allele *ca*. The terms "fast" and "slow" relate to the nature of the band separations in the electrophoresis method used for analysis. $\overline{H}_L$ = average heterozgosity per locus.

Detailed interpretation and analysis of the enzyme electrophoresis separations summarized in Table 1 will be found in Tebaldi (1982). The data presented in Table 1 are for the combined phenotypes collected at each of the two geographic locations. The numbers of phenotypes collected at each location are as follows: Battle Creek. *nikias* 21, *electa* 22, *hesperis* 1, *nikias-electa* intergrade 3. Total = 47. Cuchara Canyon. *nikias* 51, *electa* 3, *hesperis* 9, *nikias-electa* intergrade 2, *nikias-hesperis* intergrade 3. Total = 68.

Table 1. Allele Frequencies and Observed Heterozygosity per Locus for Eleven Enzyme Loci in *Speyeria atlantis* (Combined Phenotypes) from Two Localities.*

| | | **Battle Creek** | **Cuchara Canyon** |
|---|---|---|---|
| $MDH_1$ | *n* | 47 | 68 |
| | *het* | 0.00 | 0.01 |
| | *ca* | 1.00 | 0.99 |
| | *f* | — | 0.01 |
| $MDH_2$ | *n* | 47 | 68 |
| | *het* | 0.00 | 0.00 |
| | *ca* | 0.98 | 1.00 |
| | *f* | 0.02 | — |
| $ME_1$ | *n* | 46 | 52 |
| | *het* | 0.00 | 0.58 |
| | *sc* | 1.00 | 0.56 |
| | *fc* | — | 0.41 |
| | $f_1$ | — | 0.01 |
| | $f_2$ | — | 0.02 |
| $ME_2$ | *n* | 47 | 66 |
| | *het* | 0.13 | 0.14 |
| | *sc* | 0.07 | 0.20 |
| | *fc* | 0.84 | 0.66 |
| | *f* | — | 0.06 |
| | *s* | 0.09 | 0.08 |
| $ME_3$ | *n* | 46 | 67 |
| | *het* | 0.00 | 0.12 |
| | *ca* | 1.00 | 0.92 |
| | $s_1$ | — | 0.01 |
| | $s_2$ | — | 0.07 |
| *GDH* | *n* | 46 | 68 |
| | *het* | 0.04 | 0.01 |
| | *ca* | 0.98 | 0.99 |
| | *f* | 0.01 | 0.01 |
| | *s* | 0.01 | — |
| $IDH_2$ | *n* | 47 | 64 |
| | *het* | 0.00 | 0.58 |
| | *sc* | 1.00 | 0.55 |
| | *fc* | — | 0.40 |
| | *f* | — | 0.04 |
| | *s* | — | 0.01 |
| $IDH_2$ | *n* | 47 | 68 |
| | *het* | 0.02 | 0.18 |
| | *ca* | 0.99 | 0.91 |
| | *N* | 0.01 | 0.03 |
| | $s_1$ | — | 0.04 |
| | $s_2$ | — | 0.02 |
| $\alpha GPdH$ | *n* | 46 | 67 |
| | *het* | 0.02 | 0.00 |
| | *ca* | 0.99 | 1.00 |
| | *s* | 0.01 | — |
| $GOT_1$ | *n* | 47 | 68 |
| | *het* | 0.09 | 0.2 |
| | *ca* | 0.96 | 0.88 |
| | *f* | 0.02 | 0.07 |
| | *s* | 0.02 | 0.05 |
| $GOT_2$ | *n* | 45 | 67 |
| | *het* | 0.00 | 0.00 |
| | *ca* | 0.98 | 1.00 |
| | *s* | 0.02 | — |
| $\bar{H}_L$ | | 0.027 | 0.166 |

*From Tebaldi (1982).

*The Journal of Research on the Lepidoptera* 22(2): 115-117, 1983

# Occurrence of the "Elymi" Aberrant Phenotype in *Vanessa carye* (Huebner) (Nymphalidae)

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**Abstract.** A female specimen of *Vanessa carye* (Huebner) bearing the "elymi" aberrant phenotype, collected in Ancash, Perú, is reported herein. The occurrence of similar aberrant phenotypes in other species of *Vanessa* is discussed.

Natural or laboratory induced aberrant phenotypes, known as "elymi" (Shapiro, 1973, 1974), have been found in several species of *Vanessa (Cynthia)*. The first description of this particular phenotype characterized, in the words of Shapiro (1973) ". . . by suppression of the discal wing pattern, fusion of the subapical dark pattern elements, and development of a series of white submarginal spots," was given by Rambur (1829) for a specimen of *cardui* Linnaeus, collected by Rambur himself near Montpellier, France, on July 5, 1827, and regarded as a new species, which he named *Vanessa elymi*. Subsequently, a number of names (listed by Field, 1971), now recognized as infrasubspecific, were bestowed on similar aberrant individals pertaining to several other species of the genus (Table 1).

Recently, a female aberrant *Vanessa carye* (Huebner) (Fig. 1), bearing the typical "elymi" phenotype, has been collected by Enrique Pérez at

Fig. 1. Aberrant *Vanessa carye* collected in Huascarán National Park, Ancash, Peru. Upper (left) and lower surfaces. Bar = 1 cm.

Zone C of a study area in Huascarán National Park, Ancash, Peru, at 3950 m elevation, on May 26, 1981. For a description of the study area see Pérez (1982).

*Vanessa carye* is one of the commonest butterflies on the Peruvian coast and Andes, and has an extensive distribution in South America, from NW Venezuela and Colombia in the north, to Argentina and Chile in the south. It also occurs in the Juan Fernández Islands, on Easter Island and on Mangareva Island, between Chile and New Zealand (Field, 1971). Its phenotype is extremely constant in the entire distribution area, with no tendency to form subspecies. In western Peru, it may be found from sea level to the snowline (5000 m), and occurs in a great variety of habitats, from coastal deserts to relict upper montane forests and paramos. its migratory movements in western Peru have been described by Hughes (1957, 1958). The species seems to have transient populations at Huascarán National Park, where Pérez (1982) recorded dense populations in April and May 1981, during the dry season. No specimens were seen during the wet season months of August to October.

Dimock (1968) reported the induction of "elymi" phenotypes by chilling pupae of *V. cardui*. Shapiro (1973, 1974), who performed similar experiments, considered the available evidence on pupal chilling as the causative agent for the "elymi" phenotype as inconclusive, and offered instead the hypothesis that ". . . wild specimens of "elymi" are produced by genes or gene combinations which alter the threshold for expression of "elymi" so that it is produced under ordinary development conditions," and that "the occurrence of the phenotype in three species [actually, six species; cf. Table 1 in this paper]. . . suggests that it may indeed have been

**Table 1. Occurrence of "elymi" phenotypes among *Vanessa (Cynthia)* species.**

| Species | Named Aberrations |
|---|---|
| *cardui* Linnaeus | "elymi" Rambur<br>"emielymi" Verity |
| *kershawi* M'Coy | none reported |
| *virginiensis* Drury | "ahwashtee" Fox<br>"simmsi" Gunder |
| *altissima* Rosenberg &Talbot | none reported |
| *braziliensis* Moore | "dallasi" Koehler |
| *terpsichore* Philippi | none reported |
| *myrinna* Doubleday | "eunice" Hall |
| *annabella* Field | "muelleri" Letcher |
| *carye* Huebner | "caryoides" Giacomelli<br>"bruchi" Koehler |

a seasonal phenotype at one time in the evolution of the genes and that its expression was subsequently suppressed. . ."

Nightly frosts ("heladas") were reported by Pérez (1982) for his study area at Huascarán during June and July 1981, well after the probable emergence time of the aberrant specimen he collected.

Prof. José Herrera of Santiago, Chile, has collected and bred some "elymi" specimens from Chilean *V. caryae*; one such individual has recently been figured by Herrera (1982: Fig. 24).

*Acknowledgments.* I wish to thank Enrique Pérez for the information supplied on the Huascarán National Park butterfly fauna, and the donation of the "elymi" individual to the collections of the Museo de Historia Natural, Universidad de San Marcos.

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# Compilation of Data on Wing Homoeosis on Lepidoptera: Supplement I

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**Abstract.** Twenty-five mostly new examples of wing homoeosis are recorded to supplement the previously published list of wing homoeosis in Lepdioptera. They include examples of mosaics in Zygaenidae and completely bilateral posterior ventral mosaics in a papilionid species *Luehdorfia japonica*, apparently genetic mutants.

## Introduction

Further material is now available to supplement the data on wing homoeosis in Lepidoptera, as compiled by Sibatani (1983). Since the new data, and existing records which were overlooked by Sibatani (1983) contain some interesting findings, they are now reported here, insofar as they contribute to the general theory of wing homoeosis in Lepidoptera.

The additional material of 25 homoeotic examples will be recorded here in the same format as in the previous report, although the specimen number is no longer in convenient sequence for individual higher taxa. In order to provide convenience for cross references between the original and supplementary lists, a related reference number (or numbers) of the same series (B or D) in the original list is/are given in parenthesis after the new number in the following supplementary list. Extending the same reference method to the Addenda contained in the original list of Sibatani (1983), B284-B302 should read B284(14)-B302(14). Where a number such as B2+ appears, the "plus" sign signified that further information is now added to the entry B2 in the previous list. When referring to such numbers in the text, however, these additions will usually be dropped and plain numbers be used, such as B2, B302, or B304.

## List of specimens with homoeosis in Lepidoptera. Supplement I.

### 1. Fore/hindwing homoeosis

### Zygaenidae

| | |
|---|---|
| B2+ | *Zygaena occitania* de Villers ♂ France BMNH† |
| B5+ | *Zygaena filipendulae* Linnaeus ♂ UK: Queendown Warren bred 10 v Crocker BMNH† |

| | |
|---|---|
| B6+ | ______ ♂ UK: Herts., Royston 4 viii 23 T.H.L. Grosvenor BMNH† |
| B303(4) | *Zygaena carniolica* Scopoli ♂ France: Alpes Maritimes (*Oberthur*) BMNH† DLH |
| B304(5) | *Zygaena filipendulae* Linnaeus ♂ UK: Sussex, W. Horsham 18 vi 42 M. J. Heard BMNH† DVRF |
| B305(9) | *Zygaena trifolii* Esper ♂ UK: Witley 1 v 20 A. A. Tullett (*Cockayne-Kettlewell*) BMNH† DRH |
| B306(9, ?8) | ______ (? *lonicerae* Esper) ♂ No data (*Bright/Rothschild*) BMNH† WLH |

**Papilionidae**

| | |
|---|---|
| B307, 308(14, 284) | *Luehdorfia japonica* Leech ♀ Japan: Nakamura 1980: 109*(†) VLRF |
| B309(14, 284) | ______ ♀ Japan: Nagano-ken, Kitaazumi-gun, Shirouma-mura, Hosono em. 23 iv 71 (*Y. Furihata*) Nishimura *in litt.* 1982 No. 6(†) VRF |
| B310(14, 302) | *Luehdorfia puziloi* Erschoff ♂ Japan: Nagano-ken, Higashichikuma-gun, Hatamachi, Kurosawa, Sagisawa 9 iv (*Y. Fukasawa*) Nishimura *in litt.* 1982 No. 5(†) VLF |
| B311(14, 302) | ______ ♂ Japan: Nagano-ken, Kitaazumi-gun, Hakuba-mura, Moriue em. 5 iv 78 (*K. Maruyama*) Nishimura *in litt.* 1982 No. 2(†) VRLF |
| B312(14, 302) | ______ ♂ Japan: data as B311 Nishimura *in litt.* 1982 No. 1(†) VRLF |
| B313(27) | *Papilio bianor* Cramer ♂ Japan: Oshima, Nakanogo-Sumiyoshi (*Nishimura*) Nishimura *in litt.* 1982 No. 8(†) VLH |

**Pieridae**

| | |
|---|---|
| B314(35) | *Pieris brassicae* Linnaeus ♂ Europe: hybrid Canary Islands/UK; Gardiner 1963: 133* VRH |
| B315, 316(35) | ♂ data as above but not * VH |
| B317(37) | *Pieris rapae* Linnaeus ♂ Mexico: Shapiro 1983: 242 (†) VLH |
| B318(37) | ______ ♀ Mexico: Shapiro 1983:242 (†) VLH |

**Lycaenidae**

| | |
|---|---|
| B72+? | *Lycaena phlaeas* Linnaeus N. Devon; ? = *Rumicia phlaeas* UK: Cockayne 1922: 16 (North Devon [South]) VLH; N.B.—"Leech" appears in the line next to that which records *phlaeas* collected by South at "N. Devon" 1881 in *Proc. South Lond.* |

| | |
|---|---|
| | *Ent. and n.H. Soc.* 1888: 40 |
| B319(62) | *Fixenia iyonis* Ota and Kusunoki ♂ Japan: Nagano-ken, Shimoina-gun, Minamishinano-mura, Yanase em. 20 v 80 (*K. Maruyama*) Nishimura *in litt.* 1983 No. 4(†) VRH |
| B320(66) | ______ (as *Rumicia*) UK; Cockayne 1922: 16 (I. of Wight [*South*]) VH |
| B321(66) | ______ (as *Rumicia*) USA: [near New York City] 30 v 1879 E. Norstrand; Cockayne 1922: 16 VRH |
| B322(106) | *Chilades cleotas* Guérin ♀ Papua New Guinea: (*R. Mattoni*) Mattoni *in litt.* 1982 (†) VRLF |
| B323(106) | ______ ♂ Papua New Guinea: Keravat 8 x 72 (*A. Sibatani*) † VRF |

**Nymphalidae**

| | |
|---|---|
| B324(154) | *Melitaea cinxia* Linnaeus ♀ UK: Cribb 1981: 22* VLH |
| B325(162) | *Melitaea diamina* Lang ♂ S. Korea: Kwangrung 82 (*M. Nishimura*) Nishimura *in litt.* 1982 No. 9(†) VRF |
| B326(162) | ______ ♂ S. Korea: Kwangrung 17 vi 77 (*M. Nishimura*) Nishimura *in litt.* 1982 No. 10(†) VRLF |

## 2. Dorsal/ventral wing homoeosis

**Lycaenidae**

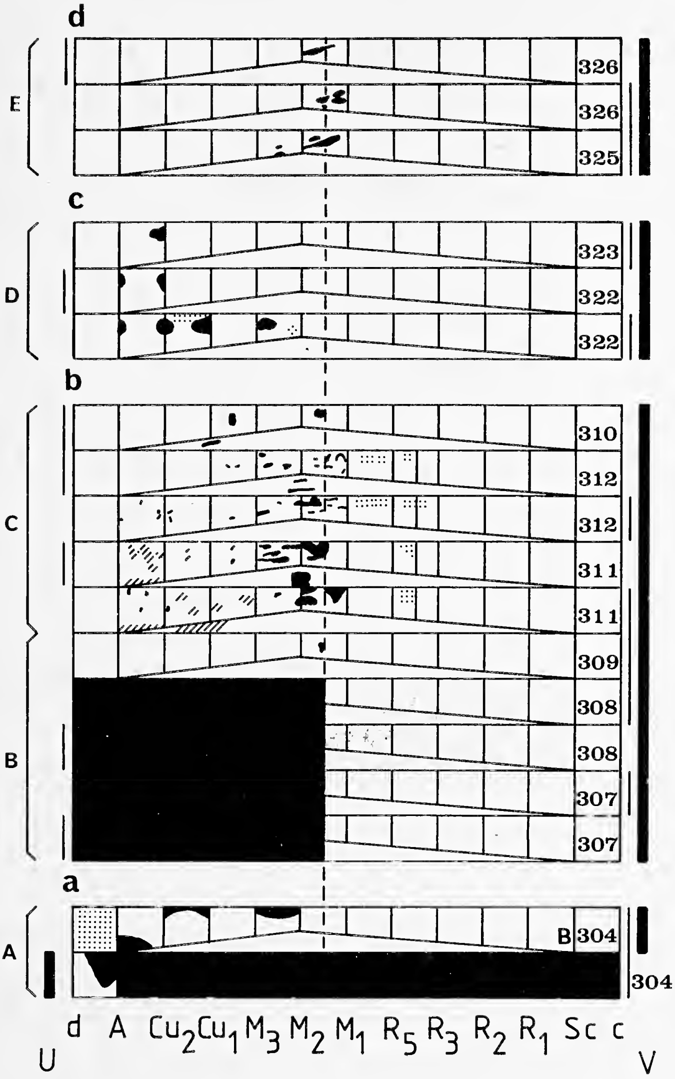
| | |
|---|---|
| D32(23) | *Lysandra coridon* Poda ♀? UK Bright and Leeds 1938: 61 (*W. Rait-Smith*) DRLF |

## Diagrammatic Representation

All the homoeosis examples included in the supplementary list and a few in the original list are illustrated in Figures 1-3 in the same diagrammatic format as given in Figures 1-12 in the previous report (Sibatani, 1983).

## Comments

1. In *Zygaenidae*, the only previously-known examples of wing homoeosis were entire fore/hindwing (F/H) conversions. We now have examples of mosaic F/H homoeosis. In *Zygaena filipendulae* B304, the dorsal surface of the right forewing is almost completely homoeotic (there being a small autotypic area along the dorsum), whereas on the ventral surface small allotypic patches are found along the termen (Fig. 1(a), A). This virtually represents a complete mosaic of the dorsal surface with its boundary slightly deviating from the wing margin. The homoeotic mosaic of *Z.*



Figs. 1-3. Maps of homoeotic mosaics in Lepidoptera wings. Supplement I. See Figs. 1-12 of Sibatani (1983) for general information about the format, symbols, etc.

Figs. 1-2. F/H homoeosis.

Fig. 1. Forewings. (a) Zygaenidae—A, *Zygaena filipendulae* Linnaeus. (b), Papilionidae—B, *Luehdorfia japonica* Leech; C, *Luehdorfia puziloi* Erschoff. (c), Lycaenidae—D, *Chilades cleotas* Guérin. (d), Nymphalidae—E, *Melitaea diamina* Lang.

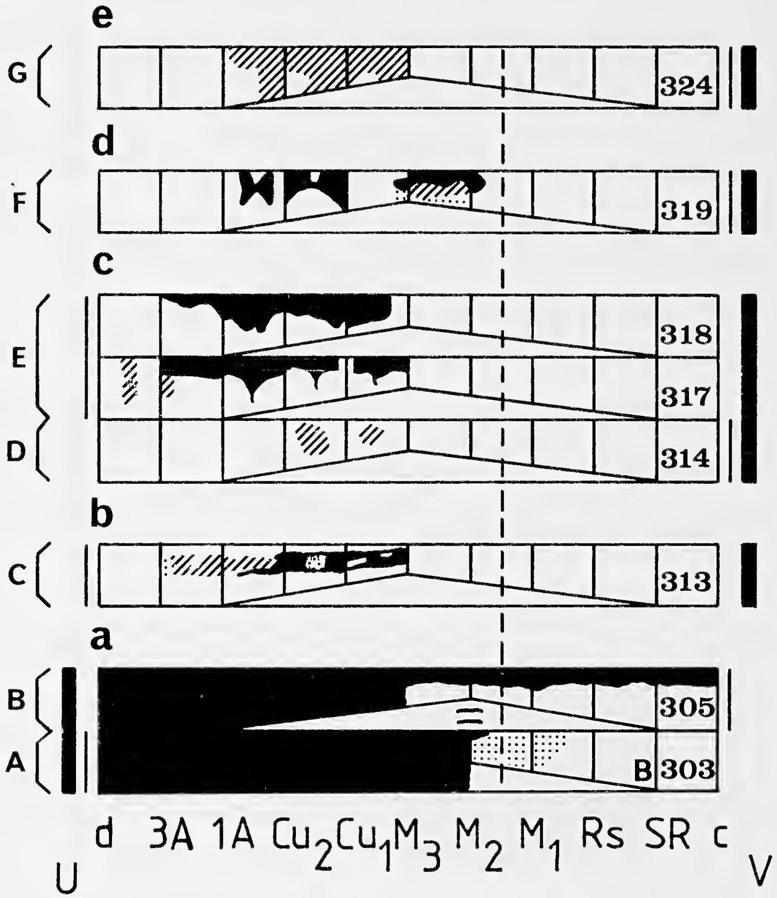


Fig. 2. Hindwings. (a), Zygaenidae—A, *Zygaena carniolica* Scopoli; B, *Zygaena trifolii* Esper. (b), Papilionidae—C, *Papilio bianor* Cramer. (c), Pieridae—D, *Pieris brassicae* Linnaeus; E, *Pieris rapae* Linnaeus. (d), Lycaenidae—F, *Fixenia iyonis* Ota and Kusunoki. (e), Nymphalidae—F, *Melitaea cinxia* Linnaeus.

*carniolica* B303 is roughly confined to the posterior half of the dorsal surface of a hindwing, whereas in *Z. trifolii* B305 part of the homoeotic patch in the posterior half of a hindwng spreads to the terminal area of the anterior half of the wing (Fig. 2(a) B,C).

2. In Papilionidae, *Luehdorfia japonica* has now provided two females having a bilaterally symmetrical complete posterior-dorsal F/H homoeotic mosaic on the forewing ventral surface (Nakamura, 1980); (Fig. 1(b), B).

The patterning on the corresponding dorsal surface is aberrant but undoubtedly autotypic. The wing form of these somewhat dwarfish specimens (Figs. 5, 6) is also subject to slight F/H-homoeotic change, showing a constriction at the autotypic/allotypic boundary along the termen. These specimens are remarkable in that the complete posterior mosaics are bilaterally symmetrical and obtained in duplicate, in the same local/seasonal population: a fact which strongly indicates that they are genetic mutants. The mosaic border runs along the midline of space $M_1$-$M_2$ and discal cell, in support of the inferred boundary of anterior and posterior compartments (Sibatani, 1980).

As Fig. 1 indicates, most of the F/H-homoeotic examples reported here represent homoeosis of the posterior half of the wing, but in *Luehdorfia puziloi* (Fig. 1(b), C) most examples show, in addition to the bulk of homoeotic patches caudad of $M_2$, minute mosaics distributed on both sides of the $M_1$-$M_2$ barrier.

3. New homoeotic examples are now recorded from the Australian region: Papua New Guinea, with a plebejine species of Lycaenidae: *Chilades cleotas*.

4. In Lycaenidae, a large number of F/H homoeoses on the ventral hindwing has been recorded for British specimens of *Lycaena phlaeas* Linnaeus (Sibatani, 1983). Not a single case of homoeosis for this common species has so far been known from Japan, although quite a number of homoeotic butterflies has been recorded from that country (Sibatani,

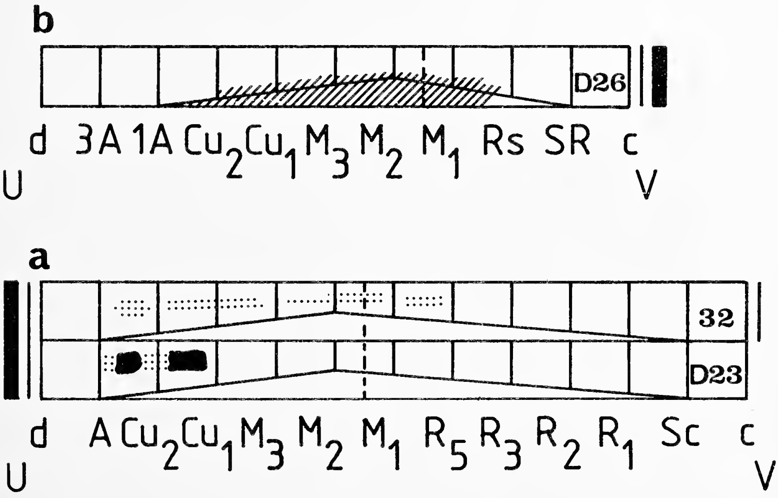


Fig. 3. D/V homoeosis: Lycaenidae—*Lysandra coridon* Poda. (a), forewings, (b), hindwing. See the list of Sibatani (1983) for D23 and D26.

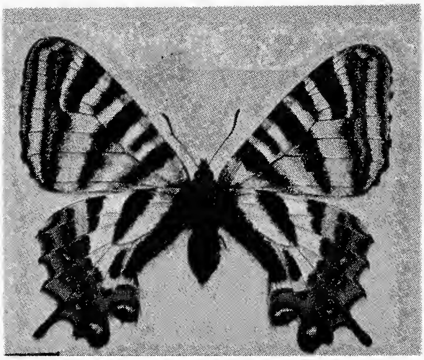


**Fig. 4.** B309

**Fig. 5.** B308.

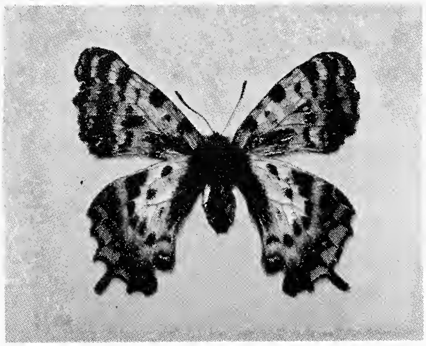


**Fig. 6.** B307.

1983). *There is one record of homoeotic* L. phlaeas *from the U.S.* (B321). Of interest therefore is the sample size of British specimens of this species among which large numbers of homoeosis were found. One such estimate is 1:500-1:1000 (Robertson, *in litt.*). I had an opportunity to examine 858 specimens of this species from Japan (mainly from Kyoto area) in the T. Minoura collection now housed at the Osaka Prefectural University School of Agriculture, but failed to find any examples of homoeosis. It would seem that the Japanese race of *L. phlaeas* is possibly less prone to become homoeotic than that in the British Isles.

5. In *Melitaea/Mellicta* (Nymphalidae), only extremely patchy mosaics on the ventral forewing have been known and these in only 3 of the European species. The same trend is now observed in a species from Korea: *Melitaea diamina* (B325, 326). However, there is now one example of *Melitaea cinxia* (B324) from U.K. which shows on the ventral surface of a hindwing an F/H conversion in a rather large mosaic patch.

*Acknowledgments.* I express my great appreciation of the assistance given me to reach and examine most of

Figs. 4-6. F/H homoeosis on the forewing ventral surface of *Luehdorfia japonica* Leech (X 0.8).

Use Fig. 4 with a very minute homoeotic patch on the right forewing (left in the figure), for the autotype patterning in comparison with allotypic areas of Figs. 5 and 6.

the new homoeotic specimens recorded here by the following institutions, colleagues and friends: The British Museum (Natural History), Osaka Prefectural University School of Agriculture, S. Ito, R. Mattoni, S. Moriuti, T. Nishimura, T. S. Robertson, A. M. Shapiro, W. G. Tremewan, R. I. Vane-Wright, and T. Yasuda. I also thank G. Johnson for the art work and Judith Howard for improvement of the manuscript.

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# Seasonality of the Butterfly Fauna in Southeastern Vietnam (Papilionoidea)

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**Abstract.** The butterfly fauna of the semi-arid savanna parts of S.E. Vietnam express a pronounced seasonality. The abundance of 49 species was recorded during the wet and dry seasons. Migratory behavior and/or slow development during the dry season seem to be frequent attributes of bionomic strategy in the monsoon seasonal climate. In some species, such as *Mycalesis* spp. and *Precis atlites* (L.), a certain type of dormancy (diapause ?) is a probable adaptation during the dry season. The insect seasonality is modified or even disappearing in wetlands, gallery forests and irrigated areas of the savanna region.

## Introduction

The western Phan Rang Plain (S. E. Vietnam) is characterized by a variety of seminatural savanna and human modified habitats conditioned by the seasonal monsoon climate. So far, the seasonality of tropical insects have been investigated in Africa (Denlinger, 1980; Owen, 1971) and in Central America (Janzen & Schoener, 1968; Wolda, 1978; Tanaka, 1982; Young, 1982). No seasonal data are available from South East Asia (cf. Seitz, et al., 1927; Corbet, Pendlebury & Eliot, 1978—with bibliography). With regard to the territory near Phan Rang, S. E. Vietnam, even basic entomofaunistic research is badly needed (see Zeleny, Spitzer & Ondracek, 1982). The aim of the present paper is to provide new data referring to insect seasonality in the tropics, particularly with regard to the monsoon climate in S. E. Asia.

## Field Observations and Records

The study was carried out during three weeks of the maximum rainfall period of the wet season (October 1980) and again at the end of the dry season (April 1982) near Nha-Ho on the Phan Rang Plain. The abundance of the butterfly families Papilionidae, Pieridae, Danaidae, Satyridae and Nymphalidae was estimated daily between 8 and 11 a.m. in the human modified savanna habitats with small patches of semideciduous monsoon forest (Table 1). On the average, the rarest species (one to five specimens per day observed) are marked by X, and the most common species (over 50 specimens) by XXX. *Melanitis leda* (L.) was observed usually in the evenings.

Table 1. Abundance of butterflies of the Phan Rang Plain, Nha-Ho, S.E. Vietnam.

| Family and Species | Wet Season October 1980 | Dry Season April 1982 |
|---|---|---|
| **Papilionidae** | | |
| *Troides aeacus* (Feld.) | XX | X |
| *Pachliopta aristolochiae* (F.) | XXX | XX |
| *Papilio demoleus* L. | X | XX |
| *Papilio polytes* L. | XX | XX |
| *Papilio memnon* L. | X | X |
| *Graphium agamemnon* (L.) | X | X |
| **Pieridae** | | |
| *Leptosia nina* (F.) | XXX | X |
| *Delias descombesi* (Bsd.) | XX | X |
| *Delias hyparte* (L.) | XX | XX |
| *Cepora nerissa* (F.) | X | O |
| *Appias libythea* (F.) | XXX | XXX |
| *Phrisura aegis* (Feld.) | X | X |
| *Ixias pyrene* (L.) | XXX | XXX |
| *Hebomoia glaucippe* (L.) | XXX | XX |
| *Pareronia anais* (Lesss.) | XXX | X |
| *Caopsilia pyranthe* (L.) | XXX | X |
| *Catopsilia pomona* (F.) | XXX | XXX |
| *Catopsilia scylla* (L.) | X | X |
| *Eurema brigitta* (Stoll) | X | X |
| *Eurema hecabe* (L.) | XXX | XXX |
| **Danaidae** | | |
| *Danaus chrysippus* (L.) | XXX | XXX |
| *Danaus genutia* (Cr.) | X | X |
| *Tirumala septentrionis* (Butl.) | XX | X |
| *Radena similis* (L.) | XXX | XX |
| *Euploea sylvestr* (F.) | X | XX |
| *Euploea mulciber* (Cr.) | O | X |
| *Euploea midamus* (L.) | XXX | XX |
| **Satyridae** | | |
| *Melanitis leda* (L.) | XX | XX |
| *Mycalesis mineus* (L.) | XXX | O |
| *Mycalesis visala* Moore | XX | O |
| **Nymphalidae** | | |
| *Ariadne ariadne* (L.) | XX | XX |
| *Vindula erota* (F.) | O ? | X |
| *Terinos clarissa* Bsd. | O | XXX |
| *Precis hedonia* (L.) | XX | O |
| *Precis atlites* (L.) | XXX | O |
| *Precis almana* (L.) | XXX | XXX |
| *Precis lemonias* (L.) | XXX | XX |
| *Precis orithya* (L.) | X | X |
| *Hypolimnas bolina* (L.) | XX | XX |
| *Neptis hylas* (L.) | XXX | XX |
| *Neptis magadha* Feld. | X | X |
| *Euthalia lubentina* (Cr.) | X | X |
| *Polyura athamas* (Drury) | X | O |
| **Riodinidae** | | |
| *Zemeros flegyas* (Cr.) | X | X |
| **Lycaenidae** (only part of the family checked) | | |
| *Castalius rosimon* (F.) | XX | XX |
| *Caleta roxus* (Godart) | X | X |
| *Zizula hylax* (F.) | XXX | X |
| *Catochrysops strabo* (F.) | XX | XX |
| *Curetis tagalica* (Feld.) | XX | X |

X = rare (1 to 5 specimens per day), X = frequent, XXX = common (over 50 specimens per day), O = no occurrence. Nomenclature from Corbet, Pendlebury & Eliot (1978).

## The Environment of the Phan Rang Plain

The investigated part of the Phan Rang Plain is a slightly elevated country, about 100-200 m altitude, situated 15-20 km to the west of the coastline of the South China Sea. The local climate is semi-arid with a long dry period from late November until April, with a limited amount of rainfall in May and June. The typical wet monsoon period near Nha-Ho is restricted mostly to October (see Schmid, 1974 and Vidal, 1979, Fig. 1).

Meteorological conditions during the periods of my butterfly investigations were in October 1980 (wet season): Air temperatures were min. 22.5° C at night, max. 33.2° C by day and mean around 27.0° C, rainfall total was 77.2 mm with a peak from 14th to 22nd October. The dry period temperatures in April 1982 were min. 22.7° C at night, max. 37.7° C by day and mean around 28.4° C. There was no rainfall after November 1981 except for a very short rain shower not exceeding 1 mm. The above meteorological data from 1980 and 1982 were supplied by the Nha-Ho Agricultural Station. A long-term climatic diagram of the coastal zone of Phan Rang was published by Schmid (1974) and Vidal (1979), showing an average annual total precipitation of 693 mm.

The vegetation of the Phan Rang Plain near Nha-Ho is described by Thai Cong Tung (1966) and briefly also by Schmid (1974). The typical formation is the lowland savanna forest and dry tropical grassland with dominant shrubs and trees of the genera *Capparis, Zizyphus, Diospyros, Albizzia* and *Calotropis*. Characteristic insect seasonality seems to be closely associated with grasses (Poaceae). Derived agro-ecosystems and ruderal habitats are supplied by the irrigation water, causing a less pronounced seasonal pattern. A great number of savanna butterflies is attracted by introduced exotic shrubs, such as *Lantana camara* L.

## Results and Discussion

Results of my observations are summarized in Table 1. A remarkable seasonality, possibly induced by a certain type of dormancy during the dry season, seems to be associated with the life cycles of *Leptosia nina* (F.), *Pareronia anais* (Less), *Mycalesis* spp., *Precis atlites* (L.) and *Polyura athamas* (Drury). Larvae of these Oriental species mostly feed on deciduous plants and the observed seasonality agrees with similar observations from the African savanna region (Owen, 1971; Larsen, Riley & Cornes, 1979; Denlinger, 1980) and from seasonal districts of Central America (Young, 1982). Remarkable alternation of abundance during the dry and wet season was not observed in the savanna species that manifest seasonal forms, e.g., in *Precis almana* (L.), *P. lemonias* (L.), *Danaus chrysippus* (L.)—associated with *Calotropis*, and *Ixias pyrene* (L.), which are probably well adapted to the semi-arid monsoon climate. Most frequently observed species, with relatively small differences in abundance during the dry and wet period (Table 1), are obligatorily associated with evergreen food plants, such as *Papilio polytes* (L.), *Pachliopta aristolochiae* (F.), *Appias lybithea* (F.), *Danaus chrysippus* (L.).

Some observed species of the genera *Catopsilia* and *Euploea* are typical migratory butterflies (see Williams, 1930). The migratory behavior of *Terinos clarissa* (Bsd.) has not been definitely recorded until now. This species was an abundant migrant at the end of dry season in late April and early May in the Phan Rang Plain (migratory movement mostly from NE to

Fig. 1. The savanna near Nha-Ho, Phan Rang Plain. Dominant shrubs are *Capparis beneolens* Gagn., *Zizyphus oenoplia* Mill. and *Diospyros chevalieri* H.Lec., October 1980, wet season.

W and SW). Migrations seem to be an important attribute of bionomic strategy in a seasonal monsoon climate.

The abundance of *Troides aeacus* (Feld.), the most remarkable Phan Rang butterfly, decreases during the dry season. This species showing a typical territorial behavior of males and many features of the stenotopic K-selection strategy, can safely survive dry seasons in relatively humid groves of gallery forests or clumps of trees with Aristolochiaceae near streams (Spitzer, 1982). In the open dry savanna, this species is often endangered by bush fire, besides other human factors. Seasonal differences in abundance were found in Macroheterocera, e.g. in some Noctuidae and Arctiidae, observed in the Phan Rang area as well. Adaptations to the savanna seasonal climate in S.E. Asia are typical for certain taxa of Lepidoptera and probably date from the last glacial pleistocene periods, as pointed out by Holloway (1982).

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# Moths of America North of Mexico, *Supplemental literature:* II

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## Fascicle 6.2, Gelechioidea, Oecophoridae

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# Conservation and Management of the Endangered Smith's Blue Butterfly, *Euphilotes enoptes smithi* (Lepidoptera: Lycaenidae)

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**Abstract.** *Euphilotes enoptes smithi* (Mattoni), commonly known as the Smith's blue butterfly (Lepidoptera: Lycaenidae), was among the first insects to be officially recognized as endangered species by the U.S. Fish & Wildlife Service. At the time of its listing in 1976, little was known about the distribution, ecology, and life history of *smithi*. Since 1977, I have intensively studied two populations at Fort Ord, a U.S. Army base near Monterey, California, using a combination of capture-recapture, life table and stage-frequency analysis techniques. Results of these studies are reviewed and preliminary management policies are discussed.

## Introduction

Six California lycaenids were recognized as endangered species (U.S. Fish & Wildlife Service, 1976; Arnold, 1981), in accordance with the Endangered Species Act of 1973 (hereafter abbreviated as ESA 1973). The Smith's Blue butterfly, *Euphilotes enoptes smithi* (Mattoni), is endemic to coastal Monterey County, California. A primary purpose of ESA 1973 is to conserve endangered ("a species which is in danger of extinction throughout all or a significant portion of its range") and threatened ("any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range") species by instituting procedures which aid their recovery and survival. However, little information was available on the distribution, environmental requirements, life history and autecology of *smithi* when it was listed. Langston (1963) listed 5 known sites where *smithi* had been collected and noted that its foodplant at these sites was *Eriogonum parvifolium* Sm. in Rees (Polygonaceae). *Eriogonum* is commonly known as buckwheat. Other published accounts have been anecdotal or casual in nature.

Effective management or conservation programs must be based on knowledge of the biological and ecological requirements of an organism. Since 1977 I have intensively studied two *smithi* populations using capture-recapture, life table, and stage-frequency analysis techniques. Results of these studies are reviewed and preliminary management policies are discussed. Conservation actions are presented in the format of a recovery plan of the Office of Endangered Species, U.S. Fish & Wildlife Service (OES/USFWS).

## Taxonomy

The Smith's Blue butterfly was originally described in the genus *Philotes* by Mattoni in 1954. Shields (1975) realigned several genera, resulting in the placement of *enoptes* in the genus *Shijimiaeoides*. The scientific name of the Smith's Blue when it was listed as an endangered species in 1976 was *Shijimiaeoides enoptes smithi*. Mattoni (1977) subsequently made a number of nomenclatural rearrangements in several genera of Scolititandini, which resulted in the placement of *enoptes* in the genus *Euphilotes*.

The following morphological characters may be used to distinguish *smithi* from other infraspecific taxa of *Euphilotes enoptes* (Fig. 1): 1) the wide marginal band on the dorsal forewings of males, 2) the faint terminal line on the underside of both wings, 3) the prominent checkering of the forewing fringe on both dorsal and ventral facies, and 4) a light underside with large, prominent macules (Langston, 1963).

## Distribution

*Euphilotes enoptes* is known from the Rocky Mountains to the Pacific Coast (Howe, 1975). Although widely distributed, colonies are usually isolated and found in association with the larval foodplant, several species of *Eriogonum*.

Mattoni (1954) described *Euphilotes enoptes smithi* from material collected by himself and Claude Smith at Burns Creek, near California State Highway 1, Monterey County, California. Two colonies were known at the time of its description. Langston (1963, 1965) noted the occurrence of several additional colonies. During 1977-1981, I systematically surveyed coastal sand dunes of Monterey County to delineate the butterfly's geographic range. It is apparent that *smithi* is more widespread than earlier believed. In addition B. Walsh (pers. comm.) and L. Turner (*in littris)* discovered *smithi* colonies in the coastal mountains of Monterey County.

Emmel and Emmel (1973) noted a population of *E. enoptes* which resembles *smithi* from the region of Ojai and Santa Paula, Ventura County. They speculate that *smithi* may possibly occur in coastal Santa Barbara County. However, R. H. T. Mattoni (pers. comm.) believes that these individuals more closely resemble *E. enoptes tildeni* Langston than *E. enoptes smithi*. Farther north, M. Smith (1978) reported a colony of *E. enoptes* near *smithi* located south of Mount Loma Prieta, Santa Cruz County. Unfortunately much of the interior coastal montane regions of Santa Cruz, Monterey, San Luis Obispo, and Santa Barbara Counties is rather inaccessible, thus there are few records from these areas. Undoubtedly numerous as yet undiscovered *smithi* colonies will be found in

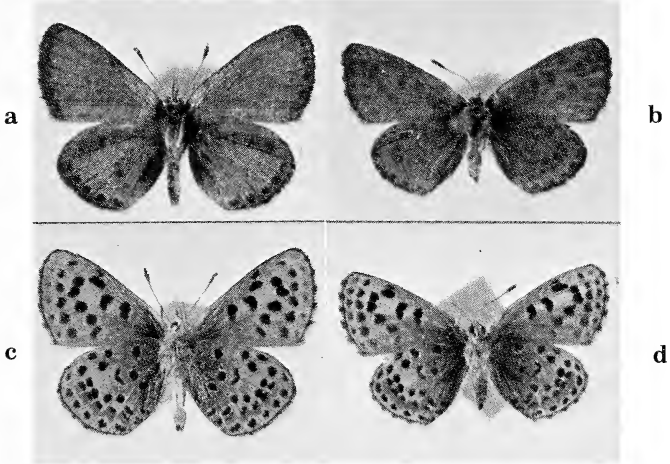
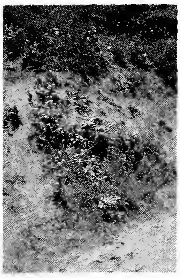


Fig. 1. Male and female of *Euphilotes enoptes smithi*: **a)** male dorsal wing facies, **b)** female dorsal wing facies, **c)** male ventral wing facies, and **d)** female ventral wing facies.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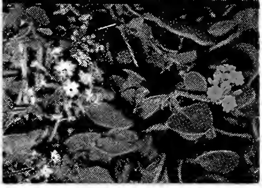
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Fig. 5. *Eriogonum latifolium*, larval and primary adult foodplant of *Euphilotes enoptes smithi* at NP.

Fig. 6. *Eriogonum parvifolium*, larval and primary adult foodplant of *Euphilotes enoptes smithi* at SP.

Fig. 7. *Mesembryanthemum edule* choking out *Eriogonum parvifolium* at SP.

Fig. 8. *Abronia latifolia* Eschs. and *A. umbellata* Lam. growing side-by-side at the California Department of Fish & Game's Ecological Reserve (locality number 13 in Fig. 2). *A. latifolia* generally has a more northern distribution while *A. umbellata* has a more southern distribution. The distribution of both species overlaps along the central California coast.

Fig. 9. Fourth instar larva of *Euphilotes enoptes smithi* feeding on *Eriogonum latifolium* flowerhead.

this region. Figure 2 depicts former and presently known localities for *Euphilotes enoptes smithi.*

## Reasons for Decline

Although *smithi*'s range is considerably greater than previously believed, significant loss and alteration of its coastal sand dune habitat has occurred through urbanization, industrialization, agriculture, recreational and military activities. Housing and commercial developments, sand-mining, and highway construction have destroyed habitat, especially on the Monterey peninsula. North of Monterey, farming (artichokes and strawberries) and recreational activities (public beaches and off-road vehicles) have destroyed or degraded habitat. At Fort Ord and elsewhere, *Mesembryanthemum edule* L., *M. chilense* Mol. and *Ammophila arenaria* (L.) Link have been planted as ground covers to stabilize the normally shifting sand dunes. Large portions of these dunes are now dominated by alien plants which hinders establishment and growth of native dune vegetation, including *Eriogonum.* In the immediate area surrounding the city of Monterey, sand dunes formerly covered approximately $600^2$ km (Powell, 1981). Over 50% of this habitat has been destroyed by man.

Coastal montane habitats for *smithi* have been less severely impacted to date because of the generally rugged and inaccessible terrain characteristic of the coastal mountains from Santa Cruz south to Santa Barbara. Nonetheless, some areas have been altered by grazing, off-road vehicle, logging and construction activities.

## Habitat Description

A coastal sand dune is one of nature's more fragile habitats. Endemic fauna and flora are extremely susceptible to habitat disruption. Powell (1981) reviewed the threats to survival for coastal California insects endemic to sand dunes, whose numbers are diminishing due to widespread loss and degradation of habitat. Dune vegetation is easily damaged by foot (Hylgaard, 1980; Hylgaard and Liddle, 1980) and vehicular traffic (Seneca, 1980).

Fig. 2. Distribution of known colonies of *Euphilotes enoptes smithi* within Monterey County, California. Colonies are numbered 1-16 as follows. Colonies in coastal canyons include **1)** 6.4 km N Pt. Gorda, **2)** 6.4 km SE Lucia, **3)** 4.8 km SE Lucia, **4)** Landells Hill-Big Creek Preserve, **5)** Burns Creek (Type Locality), **6)** Partington Canyon, and **7)** several canyons along California Highway 1 between Malpaso and Garrapta Creeks. Colonies on sand dunes include **8)** Pt. Lobos State Park, **9)** Monterey "sand hills" (extirpated), **10)** Seaside (largely extirpated), **11)** Ft. Ord, **12)** Marina Beach dunes, and **13)** California Department of Fish & Game Ecological Reserve. Colonies at inland sites include **14)** Vasquez Knob, **15)** near Carmel Valley Village, and **16)** near Paraiso Springs. State highways depicted are numbers 1, 156, and 183. Monterey County roads figured are G16 and G17. One interstate highway, 101, is noted.

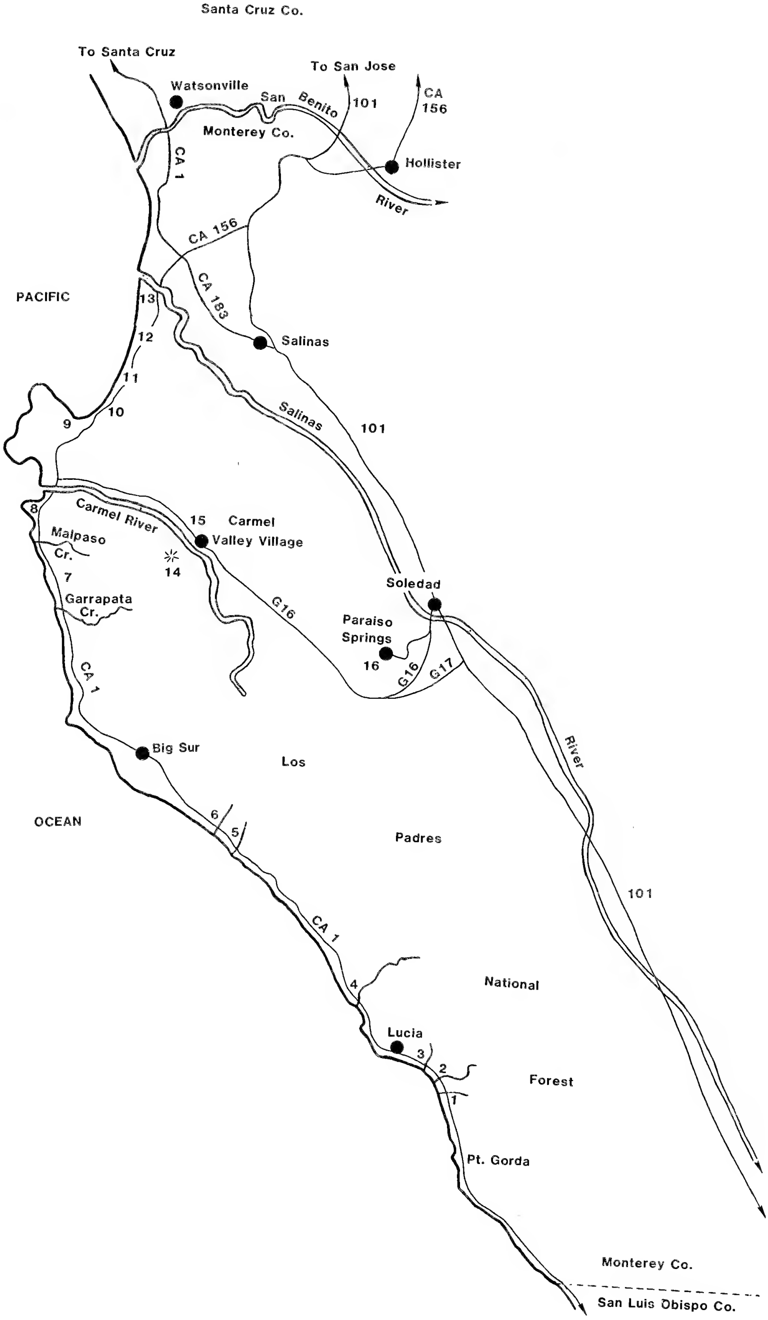
Santa Cruz Co.
To Santa Cruz
To San Jose
Watsonville
San Benito River
101
CA 156
Hollister
Monterey Co.
CA 1
CA 156
CA 183
Salinas
PACIFIC
13
12
11
10
9
Salinas River
101
8
Carmel River
15
Carmel Valley Village
Malpaso Cr.
14
7
Garrapata Cr.
Soledad
G16
Paraiso Springs
16
G16
G17
CA 1
Big Sur
Los
OCEAN
6
5
Padres
101
CA 1
4
National
Lucia
3
2
1
Forest
Pt. Gorda
Monterey Co.
San Luis Obispo Co.

Fig. 3. U.S. Army endangered species preserve sign for the northern dune preserve (study site NP) at Ft. Ord.

The formation and maintenance of a sand dune depend upon a variety of dynamic and interacting processes. Generally there are 3 zones or land forms which comprise a coastal dune: 1) foredunes, 2) deflation plain, and 3) stabilized dunes (Barbour and Johnson, 1977). At several *smithi* dune localities only 1 or 2 zones exist. The process of plant succession on Monterey peninsula dunes was described by McBride and Stone (1976).

During 1977-1981, two dune preserves at Fort Ord served as study sites for population investigations on *smithi*: the North Preserve (NP) and South Preserve (SP). These areas were designated preserves (Figs. 3, 4) in 1967 to protect examples of the natural ecosystems located on the U.S. Army base (Griffin, 1976). Fifteen rare or listed endangered plants, reptiles, and an insect are known from various preserves on the base. It was fortuitous that NP and SP became the first federal insect preserves in the United States since they were designated preserves nearly 10 years before the Smith's Blue butterfly was recognized as an endangered species.

Coastal strand plus numerous exotic species, especially *Mesembryanthemum* and *Ammophila*, comprise the dominant vegetation at these stabilized dunes (Table 1). *Eriogonum latifolium* Benth. (Fig. 5) is the foodplant for *smithi* at NP, while *E. parvifolium* (Fig. 6) is the foodplant at SP. NP is less stabilized by exotic vegetation than SP. The extent of active sand areas at both sites coincides with the location of *Eriogonum*, whereas stabilized areas correspond to the distribution of *Mesembryanthemum*, *Ammophila*, and coastal strand vegetation. Arnold (1980) gives vegetation maps for SP and NP.

Dune ecology involves a number of dynamic processes that create a balance between stability and movement of sand. Many of the woody perennial plants characteristic of dunes are dependent upon secondary deposit of aeolian sand for the establishment and growth of their seedlings. Small dune remnants frequently lack a nearby reservoir of sand and become further stabilized by weedy plants, which often outcompete endemic perennials and prevent establishment of seedlings by native

Fig. 4. **a.** U.S. Army endangered species preserve sign for the southern dune preserve (study site SP) at Ft. Ord.
**b.** Coastal strand vegetation characteristic of SP.

species, for example, allelopathic *Mesembryanthemum* (Fig. 7) species (Vivrette and Muller, 1977). *Ammophila arenaria* also outcompetes native flora. The diversity of insect life characteristically associated with native plants on natural dune systems is drastically reduced in dense stands of *Ammophila* (Slobodchikoff and Doyen, 1977).

Powell (1981) notes that along the California coastline northern dune plant communities are more mesic while southern communities are more xeric. Species diversity of dune flora is greater in northern California (13-15 species) than in southern coastal dune areas (8-10 species). Floristically, the central portion of the California coastline, particularly the Monterey area, exhibits the greatest species diversity with 20-22 species. *Eriogonum laifolium* is a member of the northern California dune flora, whereas *E. parvifolium* is representative of the southern California flora. NP is comprised of plants representing the northern dune flora. In contrast, SP which is only 5.5 km south of NP, is characterized by a southern flora.

## Life History and Behavior

*Euphilotes enoptes smithi* is univoltine. At Fort Ord, adults at study site NP emerge from mid-June until early August; at SP from mid-July until early September. Adult emergence is synchronized with the peak flowering period of *E. latifolium* at NP and *E. parvifolium* at SP. Both buckwheats are utilized as larval and adult foodplants.

Adult males and females live approximately one week. Both sexes spend the majority of their time on *Eriogonum* flowerheads either perching or obtaining nectar. Mate location, copulation and oviposition also occur on *Eriogonum* flowerheads.

There are five larval instars. Approximately one month is spent as a larva. The 3rd, 4th, and 5th instar larvae (Fig. 9) are tended by ants. For additional bionomic information consult Arnold (1978, 1980, and 1981).

Two host races or ecotypes of *E. enoptes smithi* were discerned at coastal dune areas, one feeding on *E. latifolium* and the other on *E. parvifolium* (Arnold, 1980). Peak flowering period for the former buckwheat species preceeds that of the latter by approximately 3-4 weeks. Adult emergence and larval developmental times are synchronized with the flowering period of respective foodplants. Thus the sequence of life history events for butterflies at NP and SP are partially allochronically asynchronous. Despite their geographic proximity, this phenomenon represents a potential isolating mechanism between the NP and SP populations. Future studies will be necessary to assess the effectiveness of this isolating mechanism. In other insects, similar circumstances have resulted in sympatric speciation (Bush, 1974; Tauber and Tauber, 1978).

Comparably intensive ecological studies have not been undertaken on coastal montane populations of *Euphilotes enoptes smithi*. Additional ecotypes may be found in these populations.

TABLE 1

Principal plant species at NP and SP study sites. Familial arrangement after Munz and Keck (1968).

---

*Euphorbiaceae*
- *Croton californicus* Muell-Arg.

*Papaveraceae*
- *Eschscholtzia californica* Cham. var. *maritima* (Greene) Jepson

*Cruciferae*
- *Cakile maritima* Scop.
- *Erysimum ammophilum* Heller

*Aizoaceae*
- *Mesembryanthemum chilense* Mol.
- *M. edule* L.
- *M. chilense* Mox. X *M. edule* L.

*Nyctaginaceae*
- *Abronia latifolia* Eschs.
- *A. umbellata* Lam.

*Convolvulaceae*
- *Convolvulus soldanella* L.

*Scrophulariaceae*
- *Orthocarpus purpureus* Benth. var. *pallidus* Keck
- *Castilleja latifolia* H. & A.

*Leguminosae*
- *Lupinus albifrons* Benth.
- *L. arboreus* Sims.
- *L. chamissonis* Eschs.
- *Lotus heermannii* (Dur. & Hilg.) Greene
- *Lathyrus littoralis* (Nutt. *ex* T. & G.) Endl.

*Onagraceae*
- *Camissonia cheiranthifolia* Hornem. *ex* Spreng.

*Compositae*
- *Ambrosia chamissonis* Less.
- *Artemisia pychnocephala* DC.
- *Cirsium occidentale* (Nutt.) Jepson
- *Corethrogyne leucophylla* Jepson
- *Eriophyllum staechadifolium* Lag.
- *Haplopappus eriocides* (Less.) H. & A.

*Gramineae*
- *Poa douglasii* Nees.
- *Elymus mollis* Trin. *ex* Spreng.
- *Ammophila arenaria* (L.) Link

TABLE 2

Summary of capture-recapture results on *Euphilotes enoptes smithi* during 1977-1979. The legend is as follows: numbers of individuals marked (N), residency estimates (R) (measured in days), percent of marked individuals recaptured (%R), and total estimated population numbers (TOTALS).

|  | N |  | R |  | %R |  | TOTALS |  |
|---|---|---|---|---|---|---|---|---|
| **SAMPLE** | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| 1977NP | 551 | 379 | 3.5 | 2.5 | 31.0 | 25.1 | 1777 | 1510 |
| 1978NP | 826 | 641 | 2.6 | 4.5 | 30.3 | 25.9 | 2726 | 2475 |
| 1979NP | 845 | 647 | 6.3 | 6.5 | 49.9 | 46.6 | 1693 | 1388 |
| 1978SP | 556 | 404 | 3.5 | 5.9 | 36.2 | 33.2 | 1536 | 1217 |

## Population Dynamics

Capture-recapture studies on adults were conducted during 7-18 July 1977, 27 June-12 July 1978 and 1-18 July 1979 at NP and 16-28 July 1978 at SP. Details on methodology are explained in Arnold (1980, 1982b). Data collected from these studies were used to calculate daily population numbers, lifespan (residency), vagility parameters, sex ratios, dispersion and home range (standard area of activity).

A total of 2,778 males and 2,071 females was marked during the capture-recapture studies. Each study revealed more males than females among newly captured individuals and in daily sample totals (i.e., numbers marked and recaptured). The sex ratio for the total estimated population was 57.3% males:42.7% females.

Daily NP population (males + females) estimates ranged from 97-1035 individuals in 1977, 30-1045 in 1978, and 45-1065 in 1979. Estimated total seasonal population sizes during the 3 sampling periods fluctuated between 3,000-5,200 individuals at NP (Table 2). In contrast, daily population estimates at SP, where estimated total seasonal population size was 2,753 individuals (Table 2) never exceeded 600 individuals during 1978.

Mean expected residencies indicated that females (grand mean 5.8 days) lived slightly longer than males (grand mean 4.0 days). Females might be expected to have lower average residencies due to their greater vagility. Longer movements should increase the chance that females emigrate from the study site. However both sexes are quite sedentary compared to other butterflies (Scott, 1975; Ehrlich *et al.*, 1975; Brussard and Ehrlich, 1970; Watt, *et al.*, 1977; Hafernik, 1976). Average daily movements for females were ≤47.5 m. and for males were ≤34.4 m. Approximately 75% of all observed movements were ≤23.0 m. The maximum movement for any individual was 226 m.

The home range or standard area of activity (SAA) for males ranged from 0.0-2.7 ha, with a mean for all samples of 0.9 ha. Female SAA's ranged from 0.2-3.5 ha with a mean of 1.3 ha. Approximately 2.3 ha of suitable habitat was available at NP and 4.8 ha at SP. Thus a typical male at NP utilized about 39% of the potentially occupied area, while females utilized approximately 57%. At SP, the typical male utilized about 26% and a female 35% of the total suitable habitat.

## Conservation and Management of the Smith's Blue Butterfly

Despite its recognition as a federally endangered species, the habitat of *Euphilotes enoptes smithi* continues to decline. Since the turn of the century, over 50% of the original dune habitat in the immediate Monterey area has been destroyed by man (Powell, 1981). Another and perhaps greater threat to its long-term survival on coastal dune systems is the extensive and rapid alteration of natural vegetation and dynamic features of undisturbed sand dunes by exotic plants.

One purpose of ESA 1973 is to provide a means whereby the ecosystems upon which endangered and threatened species depend may be conserved. Thus the act directs the Secretary of Interior to develop and implement recovery plans for the conservation and survival of endangered species. The recovery plan serves as a guide for governmental agencies which "justifies, delineates, and schedules those actions required for restoring and securing an endangered or threatened species as a viable self-sustaining member of its ecosystem." Now is the time to identify and implement measures necesseary to protect, maintain, and rehabilitate the unique habitats of *smithi*, before its situation deteriorates like that of its relative, *Euphilotes battoides allyni* (Shields). Unlike its congener, *Euphilotes battoides allyni*, which survives on only 33 ha at the Los Angeles International Airport and Chevron Refinery in El Segundo (Arnold, 1982a and b), populations of the Smith's Blue butterfly are distributed over an area encompassing several hundred square kilometers.

The remaining portion of this section describes actions necessary for recovery of *Euphilotes enoptes smithi*. These collective actions are herein referred to as a conservation plan, rather than a recovery plan, since this is not an official document of OES/USFWS.

## Conservation Plan for the Smith's Blue

### *Objectives and Rationale.*

*Euphilotes enoptes smithi* is classified as an endangered species by USFWS because of habitat destruction and degradation. Arresting the decline of this butterfly requires prevention of further loss or alteration of existing habitat. The primary objective of this conservation plan is to maintain known populations of *smithi* through a coordinated program of habitat preservation, rehabilitation and management. Essential requirements for the conservation of *smithi* and actions to accomplish these objectives are identified.

Integral to the conservation plan is the establishment of a management program for the Smith's Blue butterfly under which essential habitat is protected, maintained, and rehabilitated. Actions proposed to achieve these objectives are presented as a flowchart (Fig. 10). The activities proposed are divided into 5 categories: 1) protection and preservation of existing habitat sites, 2) implementation of short-term and long-term management policies, 3) development of monitoring programs to annually survey and census selected populations to determine the success of management efforts, 4) promotion of public awareness of the butterfly and its unique habitat, and 5) enforcement of federal, state, and local laws or regulations to protect *smithi*. Specific actions within each category are enumerated. Numbers in parentheses refer to specific tasks on the conservation plan flowchart (Fig. 10). These recommendations are based upon the best available information. However this conservation plan should be reviewed regularly and up-dated as new information accrues.

*Protection and Preservation of Existing Habitat.*

Several known habitat sites are owned by municipal, state or federal agencies (111, 117), e.g., Marina Beach by the City of Marina (114), Landels-Hill Big Creek reserve by the University of California (125), and Fort Ord by the U.S. Army. Several of these land owners are cognizant of the presence of *smithi* on their properties and have expressed a desire to participate in protection and management efforts. Preservation of publicly owned parcels can be arranged via cooperative agreements or memoranda of understandings (MOU's) between the agencies responsible for protection of the butterfly, USFWS and California Dept. of Fish & Game (CDFG), and respective land owners (1, 11). Privately owned habitat sites require other measures to insure their protection (114, 115, 116, 118, 119, 120, 121, 122, 123, 124). Cooperative agreements or MOU's may be sufficient to secure one or more of these sites, while purchase or conservation easements may be necessary to protect other sites.

Critical habitat for an endangered species is defined by ESA 1973 as the area containing those features essential to conservation of the species and alerts other federal agencies to the presence of an organism of concern. State or private actions that do not involve federal funding or require federal approval *may* be exempt from compliance with regulations under ESA 1973. For example, state and private concerns are exempt from compliance with Section 7 of the ESA 1973, which describes interagency cooperation and consultation processes. However, state and private concerns must comply with Section 9, Prohibited Acts, which includes killing or harming a listed endangered species. Critical habitat was proposed for *Euphilotes enoptes smithi* in February 1977, but the designation was not finalized because the time limit for a rulemaking expired. Since then several additional colonies of *smithi* have been discovered and listing requirements have been changed. Now economic as well as biological factors must be considered in proposing critical habitat. Reproposal of critical habitat (13) should probably be delayed until 1) further survey work is completed to delimit the entire range of *smithi* and its ecotypes (14), and 2) taxonomic questions regarding the Santa Barbara and Santa Cruz County populations are resolved (15).

### *Maintenance of Existing Habitat.*

White and Bratton (1980) noted that after habitats are legally protected, an array of ecological changes continue to affect species and ecosystems, including a) natural and human-induced, b) beneficial and detrimental, and c) from manageable to non-manageable. Many of the and dune, canyon and rocky hillside habitat sites of *smithi* have been altered or degraded by various factors discussed earlier. Mere protection of these sites will not be adequate to halt further large-scale ecological degradation of existing habitats. Intelligent management will be essential to preserve *Euphilotes enoptes smithi* at these sites.

A number of short- and long-term management activities will be necessary. Initially, preventive maintenance is required to sustain requisite larval and adult resoures at all known localities (12). In part, this can be accomplised by minimizing use of toxic substrates (121), ORV activity (122) and the planting of exotic vegetation (123). Long-term management activities should, in addition to the above factors, focus on rehabilitating habitat and reducing effects of other unnatural limiting factors (2, 21, 211, 2111, 214, 22). Control or removal of noxious and weedy plants which exclude *Eriogonum* and other endemics is desirable (21111). Alien plants are responsible for stabilization of much of the remaining sand dune habitat. Secondary redeposit of aeolian sands is minimal, thus natural seedling establishment of *Eriogonum* and other dunes endemic plants has been limited (Arnold, 1980; Powell, 1981). If natural reestablishment does not occur (21112), propagation and transplanting might be necessary (21112). At coastal canyon and montane sites, rock slides may be important in the establishment of *Eriogonum* seedlings. This and other perturbation factors require elucidation. Likewise, only a limited amount of information on the physical and climatic factors of habitat sites is known (2113). McBride and Stone (1976) discussed such characteristics for Monterey area sand dunes. Similar information for coastal canyon and mountainous areas is needed.

### *Additional Research.*

*Euphilotes enoptes smithi* undoubtedly occurs at several heretofore undiscovered localities in coastal canyons and mountains of Monterey

County. Due to the inaccessibility of this rugged region, a thorough ground level survey may be impossible. However, an aerial survey, performed in a helicopter at a ceiling height < 500 ft. would probably be adequate to map larger patches of *Eriogonum*. Follow-up ground reconaissance could determine the status of *smithi* at new localities (14). I suggest that the aerial survey be conducted during July and August, when *Eriogonum latifolium* and *E. parvifolium* bloom and would be most conspicuous.

The uncertain taxonomic status of *Euphilotes enoptes* populations in Santa Cruz and Santa Barbara counties must be resolved (15). If they are determined to be *smithi*, then the above mentioned survey work should be expanded to also include these regions. If these outlier populations are consubspecific, OES/USFWS might decide to downlist *smithi* to threatened species status, or remove it from the endangered species list.

Autecological research completed to date has focused on two sand dune ecotypes of *smithi* (Arnold, 1978, 1980). Similar investigations should be performed on one or more montane and canyon populations (212, 2121, 2122, 2123, 2124, 2125, 2126). Preliminary comparisons of sand dune and chaparral ecotypes revealed differences in vegetation types, density of the host *Eriogonum*, habitat size, intra- and inter-patch sizes of the *Eriogonum*, and utilization of secondary nectar resources. Differences in these characteristics are likely to influence the population structure, numbers, and dispersal abilities of *smithi* ecotypes, factors which must be understood for implementation of adequate conservation and management practices. In addition, the role of ants in protecting larvae requires further investigation (2122).

Several sand dune localities for *smithi* require extensive rehabilitation. A basic requirement for the conservation of *Euphilotes enoptes smithi* and its sand dune ecosystem is the revegetation by native plant species and the elimination of exotic flora. Study sites should be established and a variety of techniques explored to assess the most cost effective and ecologically compatible means to improve habitat conditions (2112). Research by McBride and Stone (1976) should offer preliminary guidelines. In addition, growth data on *Eriogonum* and other endemic plants are needed for propagation, rehabilitation, and management studies. Autecological studies on *Eriogonum* and selected endemic species would provide insight into propagation, rehabilitation and management efforts, and especially provide baseline data to design annual survey methods to measure the success of these efforts (213, 2131, 2132, 2133, 2134).

Due to the different characteristics of the *smithi* ecotypes, habitat sites and number of localities, the accumulated data should be utilized to devise a computer simulation model to assist in formulating management policies and optimize management strategies (221). This model would permit analyses to be performed by the computer rather than on-site and would provide valuable insight into rehabilitation and management actions.

Census techniques must be developed to periodically monitor the status of *Euphilotes enoptes smithi* with minimal expenditure of time and personnel (3, 31). Capture-recapture data of Arnold (1978, 1980, 1982b) could be used to construct a catch-per-effort model (311, 312). Craig's (1953) method for assessing population numbers, as well as other censusing techniques should be rigorously evaluated for accuracy compared to capture-recapture models of Jolly-Seber (Jolly, 1965; Seber, 1965), Manly-Parr (Manly and Parr, 1968), and Fisher-Ford (Fisher and Ford, 1947). Initially I would suggest that several methods be tested simultaneously and the results compared to estimates of capture-recapture models. After suitable census methods are devised, it would also be advisable to periodically conduct a capture-recapture study, perhaps every 4 to 5 years, to re-evaluate the accuracy of other census methods.

### *EDUCATION ACTIVITIES*

Protection of *Euphilotes enoptes smithi* plus its dune and chaparral habitats could be greatly facilitated by increased public awareness (4). Once habitat sites are secured, interpretive tours, displays and publications should be prepared and offered to the general public (41, 42, 421, 422, 423). Although this conservation plan has focused attention on the Smith's Blue butterfly, habitat protection and management combined with increased public awareness will benefit many other endemic wildlife and plant species of concern. Two rare lizards are known from sand dunes on the Monterey peninsula. The California Native Plant Society recognizes the dune endemic wallflower, *Erysimum ammophilum* Heller, as an endangered species. In the meantime, all laws and regulations which provide protection for *smithi* should be enforced (5).

Fig. 10. Conservation plan for the Smith's Blue butterfly. Although management policies refer primarily to coastal sand dune habitats, similar activities should be undertaken at the coastal canyon and inland sites.

FLOWCHART:

Prime Objectives: preserve and enhance presently known Smith's Blue Butterfly (SBB) populations in Monterey County, California, through an integrated program of habitat protection and management; survey other sites to discover additonal colonies; undertake biological studies to provide further insight with management policies.

1. Preserve, protect, and manage existing habitat to provide adequate conditions for existing SBB populations.
    11. Preserve known habitat sites by preventing further degradation, development,or environmental modification, through a) cooperative agreements, b) memoranda or understandings, c) conservation easements

between USFWS/CDFG and respective land owners, d) acquisition through purchase or donation, or e) cooperative agreement with the California Coastal Commission.

111. CDFG Ecological Preserve
112. Marina Beach dunes
113. Ft. Ord dunes
114. Seaside dunes
115. Pt. Lobos State Park
116. Vasquez Knob
117. Paraiso Springs
118. Carmel Valley
119. Burns Creek
120. 6.4 km N Pt. Gorda
121. 6.4 km SE Lucia
122. 4.8 km SE Lucia
123. Landels-Hill Big Creek Reserve
124. Partington Canyon
125. Coastal canyons between Malpaso and Garrapata Creeks

12. Maintain requisite larval and adult resources at all known habitat sites.
    121. Minimize use of herbicides, insecticides, and other toxic substances.
    122. Minimize ORV activity.
    123. Minimize plantings of exotic vegetation.
13. Propose Critical Habitat.
14. Survey additional sites along Monterey County coastline and inland areas for presence of *Eriogonum* and SBB populations, and arrange appropriate protection.
15. Clarify taxonomic status of outlier populations (i.e., Santa Cruz and Santa Barbara County *Euphilotes enoptes*).

2. Manage and enhance known SBB populations by maintaining habitat size, improving habitat quality, and reducing effects of other limiting factors.
   21. Devise and implement interim management plans.
       211. Investigate and initiate habitat improvement methods as appropriate.
            21111. Remove or control undesirable noxious and weedy plants from sites which outcompete *Eriogonum* and other dune endemic plants.
            21112. Promote natural seedling establishment of *Eriogonum* and other endemic plants.
            21113. If necessary, propagate and transplant native plants.
            2112. Conduct research to determine most ecologically compatible and cost-effective techniques for habitat improvement.

- 2113. Determine physical (ex., edaphic conditions, slope, etc.) and climatic (ex., precipitation, temperature, etc.) factors of habitat sites and relate to habitat improvement actions.

212. Conduct additional research on SBB autecology for each of the three ecotypes.
    - 2121. Life History.
    - 2122. Role of ants in protection of larvae from predators and parasites.
    - 2123. Population structure.
    - 2124. Adult behavior; mating, foraging, oviposition, etc.
    - 2125. Determine predators, parasitoids, and other limiting factors.

213. Conduct autecological research on bionomics of *Eriogonum parvifolium* and *E. latifolium*.
    - 2131. Life History.
    - 2132. Determine mortality factors.
    - 2133. Determine limiting factors, such as edaphic conditions, slope, exposure, etc.
    - 2134. Conduct horticultural studies to determine propagation techniques, if necessary.

214. Conduct autecological research on tending ant species.

22. Evaluate data and incorporate findings into the development of long-term management plans.
    - 221. Devise a computer simulation model to assist in management decisions.

3. Monitor SBB populations to determine status and success of management.
    - 31. Conduct annual surveys to monitor SBB populations.
        - 311. Develop suitable survey methods to estimate population numbers, distribution, and population trends.
        - 312. Determine sites to be surveyed.

4. Increase public awareness of SBB through education and information programs.
    - 41. Establish information signs at known habitat sites and offer interpretive tours of one or more sites.
    - 42. Establish audio and visual programs and publications.
        - 421. Prepare TV and radio spot programs.
        - 422. Prepare audio-visual display on SBB preservation and management program.
        - 423. Prepare conservation education program on SBB natural history.

5. Enforce laws and regulations to protect SBB.

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*The Journal of Research on the Lepidoptera* 22(2): 154-158, 1983

## Opinion

# Crows, Bobs, Tits, Elfs and Pixies: The Phoney "Common Name" Phenomenon

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and

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**Abstract.** Arguments are presented against use of common names by lepidopterists. Common names 1) are not universal; 2) neither serve as succinct labels nor clearly define relationships; 3) are language specific, and therefore hinder communication among scientists; and 4) often have been concocted, mainly at publishers' requests, on the assumption that laypersons cannot learn latinized names. Thus common names are also inherently insulting.

In Europe the "Scarce Swallowtail", *Graphium podalirius*, is scarcely scarce, while the "Scarce Fritillary", *Euphydryas maturna*, truly is. That's scarcely the only problem with common names. Another is that the Scarce Fritillary is a *Euphydryas*, a member of a genus scarcely called anything but "checkerspots" by North American collectors. And, in spite of their common names, the "Blue-branded King Crow", the "Malaysian Albatross", the "Painted Jezebel", the "Contiguous Swift", the "Sumatran Bob", the "Fluffy Tit", and the "Chocolate Tiger" are all just plain butterflies (Corbet and Pendlebury, 1956). In the face of such confusion, the Lepidopterists' Society has recently formed a committee to standardize and presumably stabilize common names. We argue that such a task is not only virtually impossible, but worse than useless since it lends legitimacy to the use of common names and that is against the best interests of lepidopterists.

Unfortunately, many new common names for North American butterflies have been coined recently at the request of publishers of butterfly guides. One obvious difficulty in standardizing these common names is that there are only about a dozen or so true, common names of Nearctic butterflies—ones whose use has developed naturally over time. Several of these refer to more (or less) than a single species. Amateurs and professionals alike recognize "Red Admiral" and "Painted Lady", although few use those names in preference to *Vanessa atalanta* and *V. cardui*. The "Red-spotted

Purple" and "Banded Purple" are well-known common names that apply to subspecies; "Tiger Swallowtail" is one that applies to a species group (and is most commonly applied to *Papilio glaucus*). Perhaps the *only* common names widely used by amateur and professional alike in the Nearctic region are "Monarch", "Viceroy", and "Mourning Cloak".

The rest of the so-called common names are not really common at all. Many widespread butterflies have been given several "common" names. And, many of those names are only regional in usage. Even in the literature on pest insects, where there is a tradition of using common names, ambiguity in butterfly names exists. Is *Pieris rapae* the "Small White", the "Cabbage White", or the "Cabbage Butterfly"? Is *Colias eurytheme* the "Orange Sulphur" or the "Alfalfa Butterfly"?

Common names do not serve well for either of the two functions of nomenclature: expression of relationships and communication. Inability to indicate relationships is particularly apparent in Europe where whites are both pierids and satyrines, and fritillaries are nymphalines and a riodinid (*Hamearis lucina*, the "Duke of Burgundy Fritillary"). Indeed, in Europe there are fully five genera called whites, seven genera of browns, seven of graylings, and an incredible fourteen genera called fritillaries (of course, many of these "genera" would better be considered subgenera—Ehrlich and Murphy, 1982).

Lack of communication is exemplified by some of the recently minted "common names". How many North American lepidopterists recognize the "Mimic", the "Elf", the "Pixie", the "Laure", the "Blue Wing", or the "Goldspot Aguna" (Pyle, 1981)? It also shows up in the invention of veritable phrases to identify species—*Colias nastes* has become the "Pale Arctic Clouded Yellow". Too many blues, graylings, woods, and ringlets? Make some anomalous blues, banded graylings, speckled woods and brassy ringlets. . . then to this add on top yet another word or two for the specific identity. Hence many common names do not provide the basic function of names or labels, as *succinct alternatives for descriptive phrases*. Of course, this was the original purpose of the binomen; before Linnaeus, short Latin phrases were used as designations of species.

Not surprisingly, common names are often outright misleading. For instance, the "Larger Lantana Butterfly" (Pyle, 1981), *Tmolus echion*, is the size of a dime. And, while *Melitaea deserticola* is the "Desert Fritillary", *Erebia epiphron*, not *Erebia montana*, is the "Mountain Ringlet" (Higgins and Riley, 1970).

The relationships/communication problem is further complicated when Nearctic and Palaearctic names are compared. Except for *Polygonia comma*, all North American *Polygonia* are not commas as in Europe but are anglewings. *Coenonympha* are heaths in Europe and ringlets in North America, while *Erebia* are ringlets in Europe and alpines in North America. Flying with alpines, of course, are arctics, *Oeneis*, in North

America but these are called graylings in Europe. The full extent of the discordance of Nearctic and Palaearctic names becomes apparent when viewing the common names of some genera of just two families, the Nymphalidae and the Pieridae (Figure 1).

A functional system of unambiguous Holarctic butterfly common names would necessitate wholesale changes on both sides of the Atlantic; "we" could agree to give up "Mourning Cloak" and accept "Camberwell Beauty" if "they" would drop "Small Copper" and use "American Copper". Or, if a priority system were instituted, we in North America would be subject to a complete turnover in names, including some of the very few recognizable ones. Certainly, no such thing will happen, but if it did the resulting English language specific common names would meld only the Americans and the British. There is no excuse for excluding non-English names. The Spanish should not be forced to call their commonest swallowtail "scarce" because it rarely reaches Britain.

On the other hand, English-speaking lepidopterists clearly do not have a monopoly on idiotic common names. Arguing that six other European countries had their own "nombres vulgares", Agenjo (1965) invented in a single sweep 199 Spanish common names including "Cervantes" for the only *Erynnis* in Spain, "Ajedrezada Viril" ("Virile Chequer") for *Pyrgus bellieri* because of its "gran deserrallo de su andropigio", and "Pedrico" for *H. lucina*, the only riodinine in Spain, in remembrance of successful collecting with his cousin Pedro Alfaro! Agenjo returns British chauvinism by naming *Carterocephalus palaemon* "Fronteriza" since it was known only from the Spanish-French border (indeed, it has been taken since in several locations well to the south—M. Gomez-Bustillo, pers. comm.). Germans have contributed their share of useless common names as the three widespread German *Euphydryas* well illustrate (Higgins and Riley, 1970). *Euphydryas maturna* is the "Kleiner Maivogel" ("Small May-flier") although it is not particularly small and normally flies in June and July. *Euphydryas intermedia* is the "Veilchen-Scheckenfalter" ("Violet Checkerspot") although it has neither a larval nor an adult association with that plant. Only the common name of *Euphydryas aurinia*, the "Skabiosen-Scheckenfalter" ("Scabious Checkerspot"), correctly identifies a host association!

The implicit argument of publishers—and the stated reason in Higgins and Riley (1970)—for the use of common names is that amateurs, particularly beginners, cannot learn latinized names. Why lepidopterists at any level should be subject to this insult is beyond us. Gardeners quite easily handle *Rhododendron, Eucalyptus,* and *Chrysanthemum*; birders use *Vireo* and *Junco*; and most five-year-olds know *Rhinoceros* and *Gorilla*, latinized names certainly no easier than *Papilio, .Colias*, or *Pieris*. The doltish-beginner argument is all the more ridiculous since a good number of recently manufactured common names are considerably more difficult

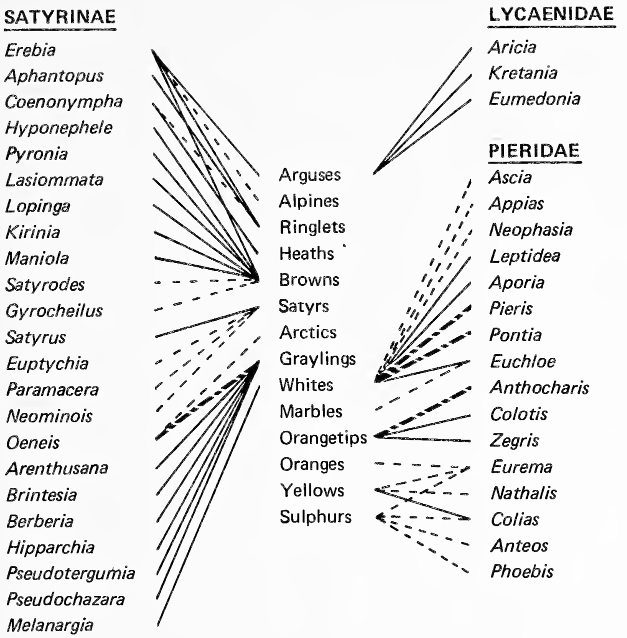

Figure 1. Illustration of the broad discordance between European (——) and North America (- - -) common names in Nymphalidae and Pieridae. A few cases of agreement are shown (▬▬▬). Note that some of the "genera" are considered subgenera by some authors.

than latinized names—in Europe *Brenthis ino* is the "Lesser Marbled Fritillary" and *Erebia nivalis* is "de Lesse's Brassy Ringlet". Still other common names are direct bastardizations of the latinized names and thus offer no advantage at all—in North America we have "Columella Hairstreaks", "Egleis Fritillaries", and "Arachne Checkerspots", among dozens of direct translations. In any case, latinized binomens are a mandatory aspect of a beginner's entry into the study and enjoyment of butterflies and are the universal currency for communication with associates, amateur and professional.

In conclusion, we appeal to the committee to stabilize common names to take as its first action its own dissolution. What needs to be done with common names is to discourage their use whenever possible. Lepidopterists should remember that, while they argue the comparative merits of worthless common names, the "Scarce Swallowtail" and the "Scarce Fritillary" are both becoming scarcer. There is so much to be learned about butterflies and so little time before so many are extinct, that to have people wasting their time haggling over whether *Xus albus* should be the

Greasy Dart or the Sleazy Tart is simply preposterous. Common names in any language should be restricted to those very few recognized by the general public, while lepidopterists should use latinized names—exclusively!

*Acknowledgments.* The insolvable confusion caused by common names became apparent over *cerveza de barril* during charter meetings of the Holarctic Lepidopterists' Union in Madrid, Spain. Both authors and the editor of this journal each claimed that the common name of *Mellicta britomartis* was, in fact, a memorial to himself.

We appreciate reviews of this note by Miguel Gomez-Bustillo, Ulf Eitschberger, Hansjurg Geiger, Richard Holm, Marian Menninger, John Thomas, and Raymond White. And, we gratefully acknowledge a gift from Daniel W. Murphy, Jr. for support of our investigations of Palaearctic *Euphydryas*.

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## Book Reviews

*Threatened Rhopalocera (butterflies) in Europe.*
Heath, J., 1981. Nature Environ. Ser. 23:i-vi, 1-157.

Very much in line with the other "red data books" this one is also divided into two distinct parts. The general part consists of chapters dealing briefly with the causes for decline divided according to their various aspects, and is supplemented with a code for collectors; further a review of conservation measures taken and proposed country by country is given (not up to date, e.g. German federal legislation not known to the author), including statistical lists of threatened species arranged country by country. Threatened species are divided into four categories (Endangered, Vulnerable, Rare, Indeterminate) and these are explained. In the special part the threatened species are listed in systematic arrangement according to the first edition (!) (1970) of the well known pocket "Field Guide to the Butterflies of Britain and Europe" by Higgins & Riley (the up-dated fourth edition published in 1980 is not mentioned); also the telegraphic data compiled on each species are by and large taken directly from the above guide, only almost always further simplified. These data include information on larval foodplants (simplified), distribution (incomplete, with some errors), habitat (very simplified, often unreliable or even useless, as on p. 50 regarding *Iphiclides podalirius* "Open country to 2000 m or above"); reasons for decline (general, putative); conservation measures taken and proposed (as a remedy it is almost always suggested to establish "large", "managed" or "suitable" nature reserves. What the author precisely means by these terms is not explained.). Lepidopterological literature suffers generally from "secondhand" statements copied usually without any reference from one book to another as well as from one author to another. How dangerous this can become is best shown by the example selected from p. 53. *Archon apollinus* is said to have world distribution "Bulgaria, Rumania, Greece and the near East" and the same is stated for its European distribution. In Bulgaria ssp. *thracica* is said to be "endangered" and in Greece an unnamed ssp. is said to be "vulnerable", no information is offered on the Rumanian populations; the reasons for decline are described as "urbanisation and possibly tourism" and as the remedy the "Establishment of suitable nature reserves" is proposed. In fact, *A. apollinus* has never been found in Rumania nor in Bulgaria; all data regarding old records of the species from Bulgaria are based on specimens found in Thracia before 1915, when this territory was briefly occupied by and annexed to Bulgaria, now a part of European Turkey, and also Greece. Also the ssp. *thracica* mentioned above was described from this area: Koru Dag Mts. in Turkey. There are some old records from the Maric (Evros) river valley and some recent records of apparently well established population(s) north of Alexandoupolis in northeastern Greece. As there is no information regarding long term development of any of these colonies, it is impossible to determine whether they have been declining; as the habitats are situated well away from larger towns and centres of tourism, it is extremely unlikely that the reasons for decline given by the author can be substantiated by facts. The foodplant is not *Aristolochia hastata* (given by Heath) but *A. bodame* and the species seems to have developed an interesting regional monophagy, apparently not known to Heath. The case of *A. apollinus* is not the only story full of errors in this book; it has been selected because it is so typical and the species is taxonomically well known, easy to find at the beginning of the special part. It would take too much space to discuss every error and put it aright, this could hardly be the objective of a short book review.

"Red data books" are by no means scientific works; their main objective is to provide the decision makers, including politicians, with elementary information on the subject. They can fulfill this purpose only if this basic information is correct and up-to-date; otherwise they are bound to fail to achieve their final aim: to help in the conservation of European fauna and flora. Compilation of a European red data book on any insect group is not an easy task; the precondition for its final success is the selection of the author, who must be thoroughly familiar with both the taxonomic group and the territory, which includes a good knowledge and understanding of the literature published in more than one language. The decision made by the "European Committee for the Conservation of Nature and Natural Resources" (Council of Europe, Strasbourg) to prepare a red data book on the threatened butterflies of Europe—to follow similar volumes on some vertebrate groups—was certainly a good idea. Unfortunately, if the final product of this idea does not fulfill the expectations of these bodies, it must be because they have set their standards very low indeed.

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*Ginace i zagrozone gatunki motyli (Lepidoptera) w faune Polski.*
Dabrowksi, J. S. & Krzywicki, M., 1982. Studia Nat. (B)31:1-171.

This "red data book" lists 62 species, from the total of 176 species, of the families Papilionidae, Pieridae, Nymphalidae, Satyridae, Hesperiidae and Zygaenidae considered under threat in Poland. Every threatened species is ranked according to the degree of decline into one of four categories: I - "potentially in danger"; II - "in danger"; III - "in great danger"; IV - "extinct". Individual monograph of each threatened species includes the following data: range distribution in Poland (with a map showing also chronologically classified extinct colonies); habitat; specific causes of decline; conservation measures proposed. Greater attention could have been paid to the community specific conservation measures. The general part deals with the habitats in Polish ecosystems, classified causes for decline (18 different aspects recognized) and types of protection measures; also the categories of threat are defined. Forestry is responsible for the decline of 42 of the total of 62 threatened species (67%) and presents thus greater threat than any other human activity; this is probably because the Polish agriculture is among the least efficient in Europe. The hygrophils form the most threatened ecological group of species within the Polish butterflies and burnets: 100% of species are considered under threat. An English summary is provided for the convenience of those unable to read and understand Polish. The book is the first of its kind ever published in a country behind the Iron Curtain and provides good basic data necessary for the launching of an efficient conservation programme for Polish butterflies and burnets. Some of the data included as well as the mode of approach is likely to be useful also outside Poland.

*Otakar Kudrna, Rhenusallee 30, D-5300 Bonn 3, West Germany*

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Cover Illustration: 1983 set of Australian stamps featuring native butterflies citing their common names.

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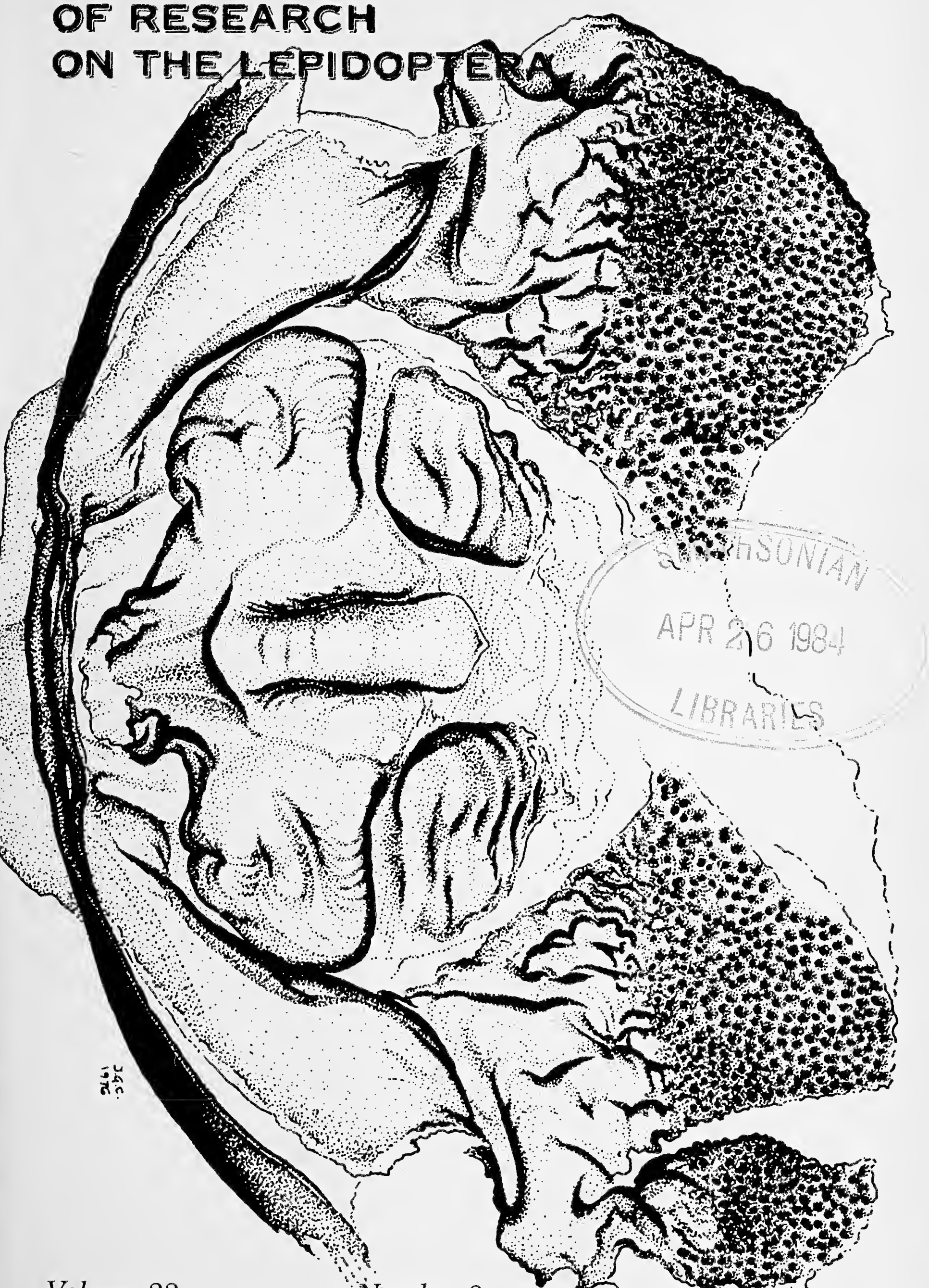

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# Description of the Female Genitalia of *Hipparchia fagi* Scopoli, *Hipparchia semele* Linnaeus (Satyridae) and their Related Taxa

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**Abstract.** The female genitalia of *Hipparchia fagi* Scopoli, *Hipparchia semele* Linnaeus and most of their related taxa are described and figured and certain aspects of their anatomy are discussed and compared. The male genitalia of these butterflies are also figured for reference purposes. Two locality maps of examined specimens are included.

## Introduction

Little information was available about the female genitalia of *H. fagi, H. semele* and their superficially similar related taxa (referred to here as the *fagi*- and *semele*-groups), until the publication of Kudrna's Revision of the Genus *Hipparchia* (Kudrna, 1977).

In this revision are figured and described the female genitalia of almost all the taxa belonging to the genus *Hipparchia*, but, despite the thoroughness of this endeavour, some of the figured genitalia are somewhat distorted, due to pressure from mounting them onto slides and some of the descriptions have missed certain aspects that may prove to be of taxonomic importance.

The purpose of the present paper is to try and rectify this situation in respect of the *fagi*- and *semele*-groups and to provide some supplementary information regarding the structure of the female genitalia of butterflies belonging to these two groups.

## Methods and Materials

The genitalia which are figured here were prepared by the usual method of overnight maceration in a 10% KOH solution, washing in water and dehydration in successive solutions of 20%, 40%, 70% and 80% ethyl alcohol. The appendages were subsequently studied and drawn while immersed in a solution of 80% ethyl alcohol, free from pressure and free to be moved about at will. Whenever necessary they were stabilized by being propped against glass slides. By the use of this method, distortion due to pressure from mounting was eliminated and a better understanding of the three dimensional structure of the appendages was achieved.

All drawings, with the exception of the explanatory diagrams, were made with the aid of a drawing tube attached to a WILD M5 stereomicroscope and were executed directly in ink, without the use of an intermediate pencil tracing. Some of these drawings are finished in detail and are often shaded, while others are mere contour studies. This discrepancy arises from the fact that often not enough time was available for their completion.

## The female genitalia (Fig. 1)

In the *Ditrysia*, which include the *Rhopalocera*, the female genitalia may be divided into two entities: a) the **Primary Genitalia**, for egg production, fertilization and laying and b) the **Bursa Copulatrix**, for sperm reception and temporary storage. The present paper deals only with the second entity.

Wherever possible, names applied to the various basic parts of the female genitalia are those in current use (Tuxen, 1970; Verity, 1953). Names for structures, or parts of structures, previously unnamed have been coined to facilitate reference to the drawings. The new names are **Post-ostial Funnel, Ventral Lamella, Dorsal Lamella, Mid-dorsal Process, Dorso-lateral Lobe, Ventral Keel, Web, Upper Flange, Lower Flange, Lateral Arm,** of **Sterigma; Bend of Ductus Bursae; Longitudinal Fold** of **Corpus Bursae**. These are given in English, or in anglicized Latin, and are descriptive and informal. It is felt that the creation of new formal names would have been meaningless, considering the poor state of our knowledge of homologies in the female genitalia.

The **Bursa Copulatrix** in the *fagi-* and *semele-*groups (Fig. 2) consists of the following parts:

1. The **Corpus Bursae,** which is a membranous, expansible sac, that receives and temporarily stores the male sperm, which, in turn, arrives enclosed in the gelatinous **Spermatophore**. The **Corpus Bursae** carries ventrally two rows of inward projecting, highly sclerotized teeth, the **Signa**, whose function, as it is generally understood, is to rupture the **Spermatophore**, thus releasing the sperm. Its outer surface bears a large number of **Longitudinal Folds**, which probably relate to its ability to expand and contract. The **Distal End of Corpus Bursae** is usually moderately sclerotized, while in some cases it may be highly sclerotized and cup-shaped. It is from this area that arises the **Ductus Seminalis,** through which sperm is transferred to the **Primary Genitalia.**

2. The **Ductus Bursae,** which is a tube, of varying degree of sclerotization, that connects the **Corpus Bursae** to the **Sterigma** and through which sperm enters the **Corpus Bursae**. It terminates distally in the **Ostium Bursae**, which is the genital opening that serves for insemination. The **Ductus Bursae** basally is angled sharply and forms the **Bend of Ductus Bursae**. In the *fagi-* and *semele-*groups it is difficult to decide

whether or not the **Ductus Bursae**, in the strict sense of the word, really exists at all; perhaps what we have here instead is what is usually referred to as an **Atrium**, which is a rather sclerotized tubular section immediately distad of the **Ductus Seminalis** and basad of the **Sterigma**, the **Ductus Bursae** being membranous and placed immediately basad of the **Ductus Seminalis** and distad of.the **Corpus Bursae**.

3. The **Sterigma** (Figs. 3 & 4), which consists of heavily sclerotized and highly modified elements, presumably derived from the 8th sternite. One of its functions may be to anchor down the **Bursa Copulatrix** to the outer abdominal wall. the **Sterigma** may be broken down into three basic units: the **Distal, Median** and **Proximal Unit**. The **Distal Unit** consists of a **Mid-dorsal Process**, two **Dorsal Lamellae**, a **Ventral Lamella** and a median section, the **Postostial Funnel**, which is directly connected basally to the **Ductus Bursae**. The **Median Unit** is composed of two **Dorso-lateral Lobes** and a mid-ventral carinate structure of I-section, the **Ventral Keel**, consisting of an **Upper** and **Lower Flange**, as well as of a perpendicular **Web**. The **Proximal Unit** consists of two **Lateral Arms** and a mid-ventral plate, the **Ventral Tray**. These three units are intricately interconnected, often by membranous tissue and form a compact and quite rigid whole.

## Description of the female genitalia

All female genitalia figured here are accompanied by illustrations of associated male appendages. This has been done in order to show correlations between the genitalia of the two sexes.

The geographic samples and total number of specimens available for study were limited, and several recognized taxa of both groups have been omitted. Thus the present study can only be considered to be a preliminary account.

The taxonomic status assigned to the various taxa of the *fagi*- and *semele*-groups is based primarily on morphological characters of the genitalia, both male and female. In the case of superficially similar, allopatric taxa it becomes anybody's guess to decide which degree of morphological differentiation in the genitalia is sufficient enough to suggest separation at species level. It thus becomes evident that the taxonomic arrangement used here is subjective and tentative.

## A. fagi-group.

### 1. *Hipparchia fagi* Scopoli 1763 (Figs. 5, 11 & 17).

Corpus Bursae flask-shaped. Length of Signa as a rule slightly over 3 mm. Distal End of Corpus Bursae lightly sclerotized. Ductus Bursae moderately sclerotized, its length being slightly over ⅓ that of Corpus Bursae; Bend of Ductus Bursae prominent and well detached from Distal End of Corpus Bursae. Mid-dorsal Process of Sterigma in dorsal view deeply concave along its longitudinal axis; distal end of this process as a rule rounded, but often with pointed tip; sides parallel to each other. Post-ostial Funnel in dorsal view with inflated sides. Dorsal Lamellae in dorsal view roughly oval, their width being about ⅓ that of Post-ostial Funnel. Area of distal half of Dorso-lateral Lobes in dorsal view at least 5 times as large as that of Dorsal Lamellae.

Material examined consists of 6 females from Greece, Macedonia, Mt. Olimbos; 5 females from Greece, Macedonia, Mt. Pangeon; 3 females from Greece, Macedonia, Mt. Falakron; 1 female from Greece, Sterea Ellas, Mt. Tymphristos; 1 female from Greece, Peloponnissos, Zachlorou; 2 females from Greece, Peloponnissos, Mt. Chelmos; 4 females from Greece, Peloponnissos, Mt. Erymanthos; 3 females from Greece, Peloponnissos, Mt. Taiyetos. No individual variation of any importance was observed.

Male genitalia: (Fig. 23)

2. *Hipparchia alcyone* Denis & Schiffermueller 1775 (Figs. 6, 12 & 18).

Corpus Bursae as in *fagi*, but smaller. Length of Signa a little under 2.5 mm. Distal End of Corpus Bursae lightly sclerotized, as in *fagi*. Ductus Bursae as in *fagi*, but half as long. Sterigma smaller than in *fagi*; Mid-dorsal Process in dorsal view as in *fagi*, but, perhaps, slightly longer. Post-ostial Funnel in dorsal view very much as in *fagi*, but somewhat smaller. Dorsal Lamellae slightly smaller than in *fagi* and rounder. Dorso-lateral Lobes smaller than in *fagi* and not as wide distally in dorsal view.

Material examined consists of 3 females from France, Vernet-les-Bains; 1 female from Czechoslovakia, Lany, Praha; 3 females from Spain, Albacete, Sierra de Alcaraz; 1 female from Spain, near Albarracin.

Male genitalia: (Fig. 24)

*H. alcyone* is separated at species level from *fagi* because of morphological differences in the male and female genitalia and because of sympatry and synchronism.

Kudrna in his revision of *Hipparchia* (Kudrna, 1977), employed the name *hermione* Linnaeus 1764, for *alcyone*, the Rock Grayling (Higgins & Riley, 1980). Higgins & Riley in a subsequent critical article on Kudrna's action (Higgins & Riley, 1978), reestablished *alcyone* Denis & Schiffermueller 1775, as the correct name for this taxon.

3. *Hipparchia syriaca syriaca* Staudinger 1871 (Figs. 7, 13 & 19).

Corpus Bursae as in *fagi*, but slightly larger. Length of Signa as a rule slightly over 3.5 mm. Distal End of Corpus Bursae and Ductus Bursae as in *fagi*, the latter being about twice as long as that of *alcyone*. Sterigma smaller than that of *alcyone*; Mid-dorsal Process in dorsal view wider at base than that of *fagi*, stubby, triangular, with pointed distal end and without the deep concavity present in *fagi* and *alcyone*. Post-ostial Funnel in dorsal view about half the size of that of *fagi*; sides not inflated. Dorsal

Lamellae about equal in size to those of *alcyone* and rather rounded in dorsal view. Dorso-lateral Lobes of about the same size as in *alcyone*, but distally not as wide in dorsal view.

Material examined consists of 10 females from Greece, Attiki, Ekali; 4 females from Greece, Attiki, Mt. Parnis; 2 females from Greece, Peloponnissos, Mt. Erymanthos; 1 female from Greece, Peloponnissos, Korfos; 1 female from Greece, Kithira island; 3 females from Greece, Samothraki island, Mt. Fengari; 1 female from Greece, Thassos island, Potamia.

Male genitalia: (Fig. 25)

*H. syriaca* has often been regarded as a subspecies of *alcyone*, by virtue of the fact that they both possess fairly similar Jullien's Organs and that they replace each other geographically (Higgins, 1975). A comparison, however, between the female genitalia of *fagi, alcyone* and *syriaca* suggests a closer affinity in some respects between the first two than between *alcyone* and *syriaca*. In view of this and the fact that *fagi* and *alcyone* are proven separate species, it would seem rather logical to have reservations about considering *syriaca* as being a subspecies of *alcyone*. Therefore, it is perhaps better regarded as a distinct species.

4. *Hipparchia syriaca ghigii* Turati 1929 (Figs. 8, 14 & 20).

The female genitalia of *ghigii* are identical with those of the nominate subspecies. This taxon is separable from the nominate subspecies on superficial grounds only (Turati, 1929).

7 females examined, all from Greece, island of Rhodes, Mt. Ataviros.

Male genitalia: (Fig. 26)

5. *Hipparchia caroli* Rothschild 1933 (Figs. 9, 15 & 21).

Corpus Bursae, Signa and Distal End of Corpus Bursae as in *fagi*. Ductus Bursae as in *alcyone*, being about half the length of that of *fagi* and *syriaca*. Sterigma about equal in size to that of *syriaca*. Mid-dorsal Process as in *syriaca*, but longer. Post-ostial Funnel in dorsal view very much as in *syriaca*, but sides somewhat more expanded. Dorsal Lamellae in dorsal view about equal in size to those of *syriaca*, but distally rather pointed. Dorso-lateral Lobes as in *syriaca*.

2 females examined, both from Morocco, Middle Atlas, Ifrane.

Male genitalia: (Fig. 27)

In some respects the female genitalia of *caroli* bear a closer resemblance to those of *syriaca* than to those of *alcyone* (Mid-dorsal Process, Post-ostial Funnel), while in others quite the opposite holds true (Ductus Bursae). Often regarded as a subspecies of the allopatric *alcyone* because of superficial similarities, as well as affinities in their respective Jullien's Organs (Higgins, 1975; Higgins & Riley, 1980). This decision is not devoid of doubt, as the female genitalia alone suggest also a close relationship to *syriaca*. At present, perhaps best regarded as a distinct species, on the basis of genitalic characters, both male and female.

6. *Hipparchia ellena* Oberthuer 1894 (Figs. 10, 16 & 22).

Corpus Bursae, Signa, Distal End of Corpus Bursae and Ductus Bursae as in *alcyone*. Sterigma of about same size as that of *syriaca* and *caroli*. Mid-dorsal Process as in *caroli*, being more pronounced than in *syriaca*. Post-ostial Funnel in dorsal view very close to that of *caroli*, but sides perhaps not quite as expanded and overall size smaller. Dorsal Lamellae in dorsal view as in *caroli*. Dorso-lateral Lobes as in *syriaca*, but perhaps somewhat wider in dorsal view.

2 females examined, both from Algeria, Batna.

Male genitalia: (Fig. 28)

The female genitalia of *ellena* on the whole seem to bear a closer affinity to those of *caroli* than to those of *alcyone*, despite the fact that superficially *caroli* is closer to *alcyone* than to *ellena*.

At present, perhaps best regarded as a separate species, on the basis of superficial, as well as genitalic characters both male and female.

## B. semele-group

1. *Hipparchia semele* Linnaeus 1758 (Figs. 29, 30, 31, 47 & 54).

Corpus Bursae about same size as that of *alcyone*, Signa slightly under 2.5 mm in length. Distal End of Corpus Bursae lightly sclerotized. Ductus Bursae moderately sclerotized; Bend of Ductus Bursae prominent and well detached from Distal End of Ductus Bursae. Sterigma smaller than in any member of the *fagi*-group; Mid-dorsal Process in dorsal view about 1½ times as long as in *fagi*, pointed and of variable width. Post-ostial Funnel shallower than in *fagi*, its width in dorsal view being about ½ that of *fagi*. Dorsal Lamellae about 2½ times as large as those of *fagi*, with rounded basal edge and straight distal edge. Dorso-lateral Lobes smaller than in any member of the *fagi*-group, their distal end in dorsal view being much narrower than in *fagi*.

Material examined consists of 1 female from England, Surrey, Woking; 1 female from Scotland, Stinchcombe, Glascow; 1 female from Scotland, Troon; 1 female from W. Scotland; 2 females from France, Fontainbleau; 1 female from France, Brittany; 1 female from Denmark, Ryjlland; 3 females from Czechoslovakia, Moravia, Mohelno; 1 female from Czechslovakia, Cermakovice; 1 female from U.S.S.R., Ukraine, Kaniev, Kiev; 2 females from Italy, Malchina, Monfalcone; 4 females from Spain, Aranjuez; 1 female from Spain, Valencia; 1 female from Yugoslavia, Croatia; 1 female from Albania, Jablanica.

Some individual variation present in the length and width of the Mid-dorsal Process of the Sterigma.

Male genitalia: (Figs. 70, 71 & 72)

The male genitalia of *semele* show a variation in size (the larger ones belonging to southern populations, while the smaller ones to northern populations), but they tend to show stability in their proportions. An exception to this rule are those belonging to Scottish specimens, which quite often have disproportionately short Brachia.

2. *Hipparchia cretica* Rebel 1916 (Figs. 32, 48 & 55).

Corpus Bursae as in *semele*, Signa about 2 mm in length, being somewhat shorter than in *semele*. Distal End of Corpus Bursae more heavily sclerotized and wider than in *semele*. Ductus Bursae at times slightly longer than in *semele* and Bend of Ductus Bursae more compressed against Distal End of Corpus Bursae. Sterigma slightly larger than in *semele*; Mid-dorsal Process and Post-ostial Funnel as in *semele*. Dorsal Lamellae and Dorso-lateral Lobes as in *semele*, but somewhat larger.

Material examined consists of 8 females from Greece, island of Crete, near Zenia; 3 females from Greece, island of Crete, Gonies.

Male genitalia: (Fig. 73)

The female genitalia of *cretica* differ only slightly from those of *semele*, quite in contrast with their respective male appendages, which exhibit between them a much greater degree of differentiation.

The pronounced disparity in size between the male genitalia of *cretica* and *semele* would tempt one to believe that, in the event of sympatry, it would be mechanically incompatible for these two taxa to copulate. The affinities between their respective female genitalia, however, tend to disprove this hypothesis.

At present, perhaps best regarded as a distinct species, primarily on the basis of characters in the male genitalia.

3. *Hipparchia mersina* Staudinger 1871 (Figs. 33, 49 & 56).

Corpus Bursae smaller than in *semele*. Signa about 1.5 mm in length, being shorter than in *semele* and *cretica*. Distal End of Corpus Bursae more heavily sclerotized than in *semele*, being as in *cretica*, but narrower than that of the latter. Ductus Bursae of about same length as that of *semele*, but Bend of Ductus Bursae rather compressed against Distal End of Corpus Bursae, as in *cretica*. Sterigma very much as in *semele*; Mid-dorsal Process, Post-ostial Funnel, Dorsal Lamellae and Dorso-lateral Lobes as in *semele*.

2 specimens examined from Turkey, Asia Minor.

Male genitalia: (Fig. 74)

The characteristic feature of the female genitalia of *mersina* is the relatively small size of the Corpus Bursae and of the Signa. Generally considered a distinct species because of minor superficial and moderate genitalic differences, as well as because of the different size and shape of the androconia (Kudrna, 1977).

4. *Hipparchia volgensis volgensis* Mazochin-Porshnjakov 1952 (Figs. 34 & 57).

Corpus Bursae and Signa as in *semele*. Distal End of Corpus Bursae unique, being highly sclerotized, wider than in all above described taxa and often cup-shaped. Bend of Ductus Bursae imperceptible, highly compressed against Distal End of Corpus Bursae and not apparent in side view. Size and shape of Sterigma as in *semele*; Mid-dorsal Process, Post-ostial Funnel, Dorsal Lamellae and Dorso-lateral Lobes as in *semele*.

Material examined consists of 1 female from U.S.S.R., near Volgograd; 2 females from U.S.S.R., Lower Volga, Krasnoarmeysk.

Male genitalia: (Fig. 75)

The characteristic features of the female genitalia of *volgensis* are the shape, high sclerotization and great width of the Distal End of Corpus Bursae, as well as the compression of the Bend of Ductus Bursae against the Distal End of Corpus Bursae. At present, perhaps best regarded as a distinct species, on account of genitalic differences, both male and female.

5. *Hipparchia volgensis delattini* Kudrna 1975 (Figs. 35, 50 & 58).

The female genitalia of *delattini* are identical with those of nominate *volgensis*. Distal End of Corpus Bursae most often cup-shaped.

Material examined consists of 3 females from Greece, Macedonia, Mt. Vermion; 7 females from Greece, Macedonia, Mt. Kaimaktsalan; 3 females from Greece, Macedonia, between Edessa and Florina; 2 females from Greece, Ipiros, Mt. Tzoumerka; 2 females from Greece, Ipiros, Mt. Siniatsiko; 3 females from Greece, Sterea Ellas, N.W. of Amphilochia; 3 females from Yugoslavia, Macedonia, Stepanci, Babuna Planina.

Male genitalia: (Fig. 76)

The similarities between *delattini* and the nominate subspecies in the female genitalia show the very close affinity between these two taxa. Separated from the nominate subspecies on the basis of minor superficial characters and small differences in the male genitalia (Kudrna, 1975; Kudrna, 1977).

The exact relationship between *delattini* and *semele* is, at present, a matter of personal conjecture, but recent evidence suggests that the two might be sympatric (thus supporting separation at species level), as their respective known distribution areas in the Balkans come very close to each other. (Southern Yugoslavia for the former and southeastern Albania for the latter).

6. *Hipparchia volgensis muelleri* Kudrna 1975 (Figs. 36, 51 & 59).

The female genitalia of *muelleri* are identical with those of *volgensis* and *delattini*, suggesting that these three taxa are very closely related to each other in this respect. The male genitalia of *muelleri*, however, appear to have features common to both *semele* on the one hand and to *volgensis* and *delattini* on the other. I have found the male genitalia of *muelleri* from the Chelmos, Peloponnissos, consistently different from those of *delattini* from northern Greece, despite individual variation in both and I do not agree with the view that the two are inseparable (Kudrna, 1977). Furthermore, all males from the Chelmos appear to have a darker upperside than does *delattini* and *volgensis*. Past evidence suggested that *muelleri* was a geographic isolate, inhabiting exclusively certain restricted areas in the Peloponnissos, Greece, but recent finds (Holloway, pers. comm.) show that possibly it also inhabits northwestern Greece, thus overlapping with *delattini*. It is my opinion that the possible record of *semele* from northwest Greece (Holloway, 1979), quite probably refers to *muelleri*. All this shows that more information is required from the Balkan area in order to form a better opinion on the distribution patterns of and the interrelationship between *muelleri* and *delattini*.

7 females and 8 males examined, all from Greece, Peloponnissos, Mt. Chelmos. Length of Mid-dorsal Process of Sterigma variable.

Male genitalia: (Fig. 77)

At present, perhaps best regarded as a subspecies of *volgensis* on the basis of minor superficial differences in the male and minor structural differences in the male genitalia.

7. *Hipparchia turcmenica* Heydemann 1942 (Figs. 37 & 60).

The female genitalia of *turcmenica* are close to those of *volgensis* and differ from them only by the narrower Distal End of Corpus Bursae and narrower Ductus Bursae.

1 female examined from U.S.S.R., Kazakhstan.

Male genitalia: not available.

At present, perhaps best regarded as a distinct species on the basis of structural characters in the genitalia, both male and female.

8. *Hipparchia pellucida pellucida* Stauder 1923 (Figs. 38 & 61).

The female genitalia of this taxon are very close to those of *volgensis*, but differ from them by the shorter and wider Ductus Bursae and the somewhat shorter Signa, being just under 2 mm in length.

Material examined consists of 3 females from Kurdistan, Sersang; 1 female from Turkey, east Anatolia, Buglan-Gecidi.

Male genitalia: not available.

The characters of the female genitalia of *pellucida* suggest a close affinity towards *volgensis* and, to a lesser extent, towards *turcmenica*.

At present, perhaps best regarded as a distinct species, on the basis of structural characters primarily in the male genitalia.

9. *Hipparchia pellucida cypriensis* Holik 1949 (Figs. 39, 52 & 62).

The female genitalia of *cypriensis* are identical with those of the nominate subspecies, thus showing, together with the characters of the male genitalia, the very close relationship between the two.

4 specimens examined from Cyprus, Mt. Kornos, near Larnaka Lapithou.

Male genitalia: (Figs. 78 & 79)

Separable from the nominate subspecies on the basis of superficial characters present both in the male and the female (Kudrna, 1977).

10. *Hipparchia aristaeus aristaeus* Bonelli 1826 (Figs. 40, 41, 63 & 64).

Corpus Bursae larger than in all above mentioned *semele*-group taxa. Signa slightly under 3 mm in length, being longer than in all above mentioned *semele*-group taxa. Overall size of Sterigma smaller than in *semele*; Dorsal Lamellae considerably smaller than in *semele*, having about ⅓ the area of those of *semele*; Mid-dorsal Process in dorsal view about ½ as long as in *semele*, as a rule wider at base than in *semele* and more or less triangular in shape. Post-ostial Funnel deeper than in *semele*. Ductus Bursae somewhat more heavily sclerotized than in *semele*. Distal End of Corpus Bursae as in *semele*, but slightly more heavily sclerotized. Bend of Ductus Bursae prominent and well detached from Distal End of Corpus Bursae, much as in *semele*.

Material examined consists of 2 females from Sardinia, Bolotana; 1 female from Sardinia, Carbonia; 2 females from Corsica, Lano; 1 female from Corsica, La Joce.

Male genitalia: (Figs. 80 & 81)

The female genitalia of *aristaeus* are characterized by the relative size of the Dorsal Lamellae, being smaller than in all above mentioned *semele*-group taxa and by the relative length and width of the Mid-dorsal Process of the Sterigma, being both shorter and wider at base than in all above mentioned *semele*-group taxa. In at least two respects, namely the Bend of Ductus Bursae and the Distal End of Corpus Bursae, *aristaeus* seems to be more closely allied to *semele* than are either *volgensis*, *pellucida*, or *turcmenica*. On the other hand the Sterigma of all these taxa is much closer to that of *semele* than is the Sterigma of *aristaeus*.

Regarded as a distinct species on the basis of pronounced morphological differences both in the male and female genitalia.

Kudrna in his revision of *Hipparchia* (Kudrna, 1977) used the name *algirica* Oberthuer 1876 for *aristaeus*. Tremewan in a book review of Kudrna (Tremewan, 1978) criticizes Kudrna's action and explains the reasons for retaining *aristaeus* as the proper name for this taxon.

11. *Hipparchia aristaeus algirica* Oberthuer 1876 (Figs. 42 & 65).

The female genitalia are identical with those of the nominate subspecies.

3 females examined, all from Morocco, Middle Atlas, Ifrane; 1 female from Algeria, Sebdou.

Male genitalia: (Fig. 82)

Separable from the nominate subspecies on the basis of superficial characters, both male and female (Higgins & Riley, 1980; Kudrna, 1977).

12. *Hipparchia aristaeus maderensis* Bethune-Baker 1891 (Figs. 43 & 66).

The female genitalia are identical with those of the nominate subspecies and those of *algirica*.

12 females examined, all from Madeira, Monte.

Male genitalia: (Fig. 83)

Separable from the nominate subspecies and from subspecies *algirica*, on the basis of superficial characters, both male and female (Higgins & Riley, 1980; Kudrna, 1977), as well as on the basis of slight morphological characters in the male genitalia (Kudrna, 1977).

13. *Hipparchia aristaeus blachieri* Fruhstorfer 1908 (Figs. 44 & 67).

Corpus Bursae larger than that of nominate subspecies. Signa just over 3 mm in length, being somewhat longer than in nominate subspecies. Overall size of Sterigma intermediate between that of *semele* and of the nominate subspecies. In all other characters identical with nominate subspecies; Dorsal Lamellae perhaps, at times, slightly larger than in nominate subspecies, but smaller than in *semele*.

Material examined consists of 2 females from Sicily, Ficuzza; 1 female from Sicily, Cefalu.

Male genitalia: (Fig. 84)

The genitalia of *blachieri*, both male and female, though bearing close affinities to those of the nominate subspecies, do, however, exhibit a certain degree of differentiation from them. This taxon is sympatric and synchronic with *semele* and, therefore, positively separated from it at the species level. Also separable from the nominate subspecies and from subspecies *algirica* and *maderensis* on the basis of superficial characters, both male and female (Higgins & Riley, 1980; Kudrna, 1977).

14. *Hipparchia aristaeus senthes* Fruhstorfer 1908 (Figs. 45, 53 & 68).

The female genitalia of *senthes* are very close to those of *blachieri*, but differ from them by the rather shorter Signa, being slightly over 2.5 mm in length, and by the somewhat shallower Post-ostial Funnel.

Material examined consists of 1 female from Greece, Sterea Ellas, near Arahova; 2 females from Greece, Sterea Ellas, Mt. Parnassos; 2 females from Greece, Attiki, Mt. Parnis; 1 female from Greece, Attiki, Ekali; 1 female from Greece, Attiki, Sounion; 1 female from Greece, Attiki, near Athens; 3 females from Greece, Hydra island; 1 female from Greece, Spetses island; 2 females from Greece, Aegina island; 3 females from Greece, Paros island; 1 female from Turkey, Anatolia, near Ankara. Some minor individual variation observed in the size and shape of the Mid-dorsal Process of the Sterigma. In Greece sympatric and synchronic with *delattini*; in Asia Minor and its Greek offshore islands, sympatric and synchronic with *mersina*, and, therefore, positively separated from both at species level.

Male genitalia: (Fig. 85)

This subspecies of *aristaeus* seems to be even more differentiated from the nominate subspecies than is *blachieri*. Separable from all above mentioned subspecies of *aristaeus* on the basis of superficial characters, both male and female (Higgins & Riley, 1980; Kudrna, 1977), as well as on the basis of minor morphological characters both in the male and female genitalia.

15. *Hipparchia azorina* Strecker 1899 (Figs. 46 & 69).

Overall size of Sterigma smaller than in *aristaeus*. Dorsal Lamellae about half as large as in *aristaeus*, or less. Mid-dorsal Process of Sterigma and Post-ostial Funnel very much as in *aristaeus*. Corpus Bursae about half the size of that of *aristaeus*. Signa shorter than in all above mentioned *semele*-group taxa, being slightly over 1 mm in length. Distal End of Corpus Bursae very lightly sclerotized. Ductus Bursae shorter than in all other *semele*-group taxa; Bend of Ductus Bursae well defined and clearly detached from Distal End of Corpus Bursae.

2 females examined from the Azores, Fayal; 1 female from the Azores, San Jorge.

Male genitalia: (Fig. 86)

The genitalia of *azorina,* both male and female, bear closer affinities to those of *aristaeus* and its subspecies than they do to those of the other taxa of the *semele*-group, thus suggesting its closer relationship to the *aristaeus* complex. Although *azorina* is sometimes regarded as a subspecies of *aristaeus* (Higgins, 1975), it is best regarded as a distinct species both on the basis of pronounced superficial differences in both male and female and because of morphological characters present in the male and female genitalia. See Oehmig (1983) for further discussion.

## The female abdominal Sphragis

The existence of a Sphragis on the abdominal tip of female *H. cretica* was first observed and figured by Higgins (1973). The present author found the Sphragis present only in individuals that also had a Spermatophore inside the Corpus Bursae, suggesting that it is associated with copulation, much as in the genus *Parnassius*. The Sphragis occurs in *semele, volgensis, delattini* and *muelleri* as a barely visible appendage, while in *pellucida, cypriensis* and *cretica*, as a prominent carinate structure. None whatsoever was found to exist in any of the subspecies of *aristaeus* and in *azorina,* while in the case of *mersina* and *turcmenica* the available females turned out to be virgins, thus precluding judgment as to the existence or not of such an appendage. it is interesting to note that affinities based on the female genitalia do not always seem to agree with those based on the Sphragis.

Two maps showing distribution of the *H. semele* and *H. fagi* taxa are given as Figures 87 and 88.

*Acknowledgments.* In conclusion I would like to extend my thanks to R. F. Bretherton, John Brown, Sir John Dacie and L. G. Higgins for their invaluable help in providing a good many of the specimens used for the present paper. I am also very grateful to R. I. Vane-Wright for his kindness to read through this paper in its original form, suggesting many corrections and improvements. I would also like to extend my thanks to J. D. Holloway, who had the kindness to show me his slides of the male genitalia of *semele*-group specimens recorded by himself during a collecting expedition in northwest Greece. Comments of an anonymous reviewer are also acknowledged.

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Diagrammatic drawing of:

**Fig. 1.** Generalized genitalia of a female butterfly.

**Fig. 2.** **Bursa Copulatrix** of a *fagi-*, or *semele*-group female butterfly.

**Fig. 3.** Exploded view of the **Sterigma** of a *fagi-*, or *semele*-group female butterfly.

**Fig. 4.** Dorsal view of the **Sterigma** of a *fagi-*, or *semele*-group female butterfly.

Side view of **Bursa Copulatrix (Sterigma** removed) of:

**Fig. 5.** *Hipparchia fagi* Scopoli. Greece, Macedonia, Mt. Olimbos, 600-800 m, 23 July.

**Fig. 6.** *Hipparchia alcyone* Denis & Schiffermueller. Czechoslovakia, Lany, Praha.

**Fig. 7.** *Hipparchia syriaca syriaca* Staudinger. Greece, Attiki, Ekali, 25 August.

**Fig. 8.** *Hipparchia syriaca ghigii* Turati. Greece, island of Rhodes, Mt. Ataviros, 450 m, 4 June.
**Fig. 9.** *Hipparchia caroli* Rothschild. Morocco, Middle Atlas, Ifrane, 3400 ft., 12 June.
**Fig. 10.** *Hipparchia ellena* Oberthuer. Algeria, Batna, August.

Side view of **Ductus Bursae** of:

**Fig. 11.** *Hipparchia fagi* Scopoli. Greece, Macedonia, Mt. Olimbos, 600-800 m, 23 July.
**Fig. 12.** *Hipparchia alcyone* Denis & Schiffermueller. France, Vernet-les-Bains, August.
**Fig. 13.** *Hipparchia syriaca syriaca* Staudinger. Greece, Attiki, Ekali, 25 August.
**Fig. 14.** *Hipparchia syriaca ghigii* Turati. Greece, island of Rhodes, Mt. Ataviros, 450 m, 4 June.
**Fig. 15.** *Hipparchia caroli* Rothschild. Morocco, Middle Atlas, Ifrane, 3400 ft., 12 June.
**Fig. 16.** *Hipparchia ellena* Oberthuer. Algeria, Batna, August.

Dorsal view of **Sterigma** of:

**Fig. 17.** *Hipparchia fagi* Scopoli. Greece, Macedonia, Mt. Pangeon, 1600 m, 26 July.
**Fig. 18.** *Hipparchia alcyone* Denis & Schiffermueller. France, Vernet-les-Bains, 19 August.
**Fig. 19.** *Hipparchia syriaca syriaca* Staudinger. Greece, Attiki, Ekali, 27 July.
**Fig. 20.** *Hipparchia syriaca ghigii* Turati. Greece, island of Rhodes, Mt. Ataviros, 450 m, 4 June.
**Fig. 21.** *Hipparchia caroli* Rothschild. Morocco, Middle Atlas, Ifrane, 3400 ft., 12 June.
**Fig. 22.** *Hipparchia ellena* Oberthuer. Algeria, Batna, August.

Side view of male genitalia (right **Valva** removed) of:

**Fig. 23.** *Hipparchia fagi* Scopoli. Greece, Peloponnissos, Mt. Taiyetos, 800-1000 m, 23 July.
**Fig. 24.** *Hipparchia alcyone* Denis & Schiffermueller. Austria, Steinfeld, 10 July.
**Fig. 25.** *Hipparchia syriaca syriaca* Staudinger. Greece, Attiki, Ekali, 12 July (**Penis** detached).
**Fig. 26.** *Hipparchia syriaca ghigii* Turati. Greece, island of Rhodes, Mt. Ataviros, 450 m, 2 June.
**Fig. 27.** *Hipparchia caroli* Rothschild. Morocco, Middle Atlas, 6500 ft., September (**Penis** detached).
**Fig. 28.** *Hipparchia ellena* Oberthuer. Algeria, Lambese, June (**Penis** detached).

Side view of **Bursa Copulatrix** (**Sterigma** removed) of:

**Fig. 29.** *Hipparchia semele* Linnaeus. Denmark, Ryjlland, 7 August.
**Fig. 30.** *Hipparchia semele* Linnaeus. W. Scotland, July.
**Fig. 31.** *Hipparchia semele* Linnaeus. Albania, Jablanica, June.
**Fig. 32.** *Hipparchia cretica* Rebel. Greece, island of Crete, near Zenia, 800 m, 14 June. (Seemingly excessive length of **Ductus Bursae** due to fact that part of **Post-ostial Funnel** of **Sterigma** accidentally left attached to it.)

**Fig. 33.** *Hipparchia mersina* Staudinger. Turkey, Asia Minor.
**Fig. 34.** *Hipparchia volgensis volgensis* Mazochin-Porshnjakov. U.S.S.R., Krasnoarmeysk, Lower Volga.
**Fig. 35.** *Hipparchia volgensis delattini* Kudrna. Yugoslavia, Macedonia, Stepanci, Babuna, July.
**Fig. 36.** *Hipparchia volgensis muelleri* Kudrna. Greece, Peloponnissos, Mt. Chelmos, 1300 m, 24 July.
**Fig. 37.** *Hipparchia turcmenica* Heydemann. U.S.S.R., Kazakhstan, Zaysan, upper Irtysh.
**Fig. 38.** *Hipparchia pellucida pellucida* Stauder. Iraq, Kurdistan, Sersang, 3500 ft., 27 May.
**Fig. 39.** *Hipparchia pellucida cypriensis* Holik. Cyprus, Mt. Kornos, near Larnaka Lapithou, 310 m, 28 April.
**Fig. 40.** *Hipparchia aristaeus aristaeus* Bonelli. Corsica, La Joce, 6 August.
**Fig. 41.** *Hipparchia aristaeus aristaeus* Bonelli. Sardinia, Carbonia, 20 July.
**Fig. 42.** *Hipparchia aristaeus algirica* Oberthuer. Algeria, Sebdou.
**Fig. 43.** *Hipparchia aristaeus maderensis* Baker. Madeira, Monte.
**Fig. 44.** *Hipparchia aristaeus blachieri* Fruhstorfer. Italy, Sicily, Ficuzza, 2300 ft., 29 June.
**Fig. 45.** *Hipparchia aristaeus senthes* Fruhstorfer. Greece, Attiki, near Athens.
**Fig. 46.** *Hipparchia azorina* Strecker. Azores, San Jorge, 8 September.

Side view of **Ductus Bursae** of:

**Fig. 47.** *Hipparchia semele* Linnaeus. Albania, Jablanica, June.
**Fig. 48.** *Hipparchia cretica* Rebel. Greece, island of Crete, near Zenia, 800 m, 14 June.
**Fig. 49.** *Hipparchia mersina* Staudinger. Turkey, Asia Minor.
**Fig. 50.** *Hipparchia volgensis delattini* Kudrna. Greece, Macedonia, Mt. Vermion, 1000 m, 24 July.
**Fig. 51.** *Hipparchia volgensis muelleri* Kudrna. Greece, Peloponnissos, Mt. Chelmos, 1300 m, 24 July.
**Fig. 52.** *Hipparchia pellucida cypriensis* Holik. Cyprus, Mt. Kornos, near Larnaka Lapithou, 310 m, 28 April.
**Fig. 53.** *Hipparchia aristaeus senthes* Fruhstorfer. Greece, Attiki, Mt. Parnis, 6 June.

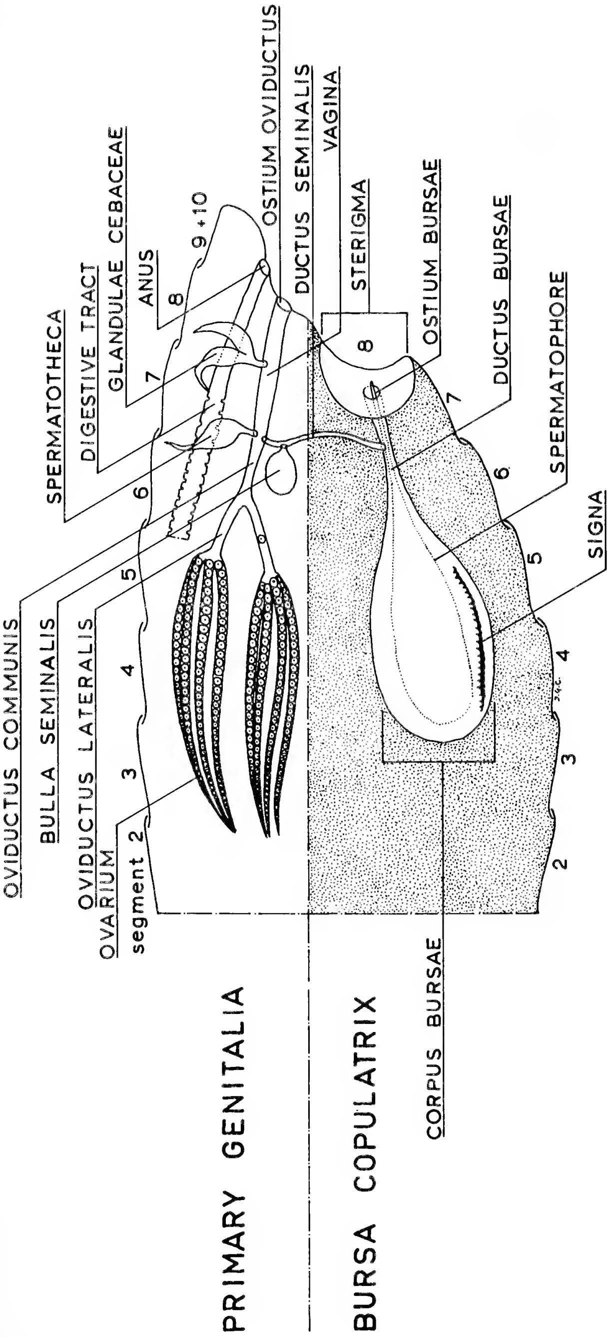
Dorsal view of **Sterigma** of:

**Fig. 54.** *Hipparchia semele* Linnaeus. Spain, Aranjuez, 1500 ft., 29 April.
**Fig. 55.** *Hipparchia cretica* Rebel. Greece, island of Crete, near Zenia, 800 m, 14 June.
**Fig. 56.** *Hipparchia mersina* Staudinger. Turkey, Asia Minor.
**Fig. 57.** *Hipparchia volgensis volgensis* Mazochin-Porshnjakov. U.S.S.R., Krasnoarmeysk, Lower Volga.
**Fig. 58.** *Hipparchia volgensis delattini* Kudrna. Greece, Macedonia, Mt. Vermion, 1000 m, 24 July.
**Fig. 59.** *Hipparchia volgensis muelleri* Kudrna. Greece, Peloponnissos, Mt. Chelmos, 1300 m, 24 July.
**Fig. 60.** *Hipparchia turcmenica* Heydemann. U.S.S.R., Kazakhstan, Zaysan, upper Irtysh.

**Fig. 61.** *Hipparchia pellucida pellucida* Staudinger. Iraq, Kurdistan, Sersang, 3500 ft., 27 May.
**Fig. 62.** *Hipparchia pellucida cypriensis* Holik. Cyprus, Mt. Kornos, near Larnaka Lapithou, 310 m, 28 April.
**Fig. 63.** *Hipparchia aristaeus aristaeus* Bonelli. Corsica, La Joce, 6 August.
**Fig. 64.** *Hipparchia aristaeus aristaeus* Bonelli. Sardinia, Carbonia, 20 July.
**Fig. 65.** *Hipparchia aristaeus algirica* Oberthuer. Algeria, Sebdou.
**Fig. 66.** *Hipparchia aristaeus maderensis* Baker. Madeira, Monte.
**Fig. 67.** *Hipparchia aristaeus blachieri* Fruhstorfer. Italy, Sicily, Cefalu, 2500 ft., 13 July.
**Fig. 68.** *Hipparchia aristaeus senthes* Fruhstorfer. Greece, Attiki, near Athens.
**Fig. 69.** *Hipparchia azorina* Strecker. Azores, San Jorge, 8 September.

Side view of male genitalia (unless otherwise stated, right **Valva** removed) of:

**Fig. 70.** *Hipparchia semele* Linnaeus. Spain, Albarracin, July (**Setae** not shown).
**Fig. 71.** *Hipparchia semele* Linnaeus. Albania, Jablanica, June (**Setae** not shown, left **Valva** removed, **Penis** detached).
**Fig. 72.** *Hipparchia semele* Linnaeus. Scotland, July (**Setae** not shown).
**Fig. 73.** *Hipparchia cretica* Rebel. Greece, island of Crete, Aghios Nikolaos, sea level, October.
**Fig. 74.** *Hipparchia mersina* Staudinger. Turkey, Antalya, 4000 ft., 16 June.
**Fig. 75.** *Hipparchia volgensis volgensis* Mazochin-Porshnjakov. U.S.S.R., Krasnoarmeysk, Lower Volga (**Penis** detached).
**Fig. 76.** *Hipparchia volgensis delattini* Kudrna. Greece, Macedonia, between Edessa and Florina, 4 July (**Setae** not shown).
**Fig. 77.** *Hipparchia volgensis muelleri* Kudrna. Greece, Peloponnissos, Mt. Chelmos, 1400 m, 15 July. (**Setae** not shown, **Penis** detached; this individual has a **Valva** that is close to that of *semele* and is rather exceptional; usually the **Valva** is intermediate between that of *semele* and nominate *volgensis*).
**Fig. 78.** *Hipparchia pellucida cypriensis* Holik. Cyprus, Mt. Pentadaktylos, April. (**Penis** detached, left **Valva** tilted outward and, therefore, presenting distorted view.)
**Fig. 79.** *Hipparchia pellucida cypriensis* Holik. Cyprus, Mt. Pentadactylos, near Halevga, 450 m, 29 April (side view of left **Valva**; **Setae** not shown).
**Fig. 80.** *Hipparchia aristaeus aristaeus* Bonelli. Corsica Lano, 1000 m, 13 July (left **Valva** removed, **Penis** detached).
**Fig. 81.** *Hipparchia aristaeus aristaeus* Bonelli. Sardinia (**Setae** not shown).
**Fig. 82.** *Hipparchia aristaeus algirica* Oberthuer. Algeria, Anosseur, Middle Atlas, 14 May.
**Fig. 83.** *Hipparchia aristaeus maderensis* Baker. Madeira (**Penis** detached).
**Fig. 84.** *Hipparchia aristaeus blachieri* Fruhstorfer. Italy, Sicily, Cefalu, 2500 ft., 13 July (**Penis** detached).
**Fig. 85.** *Hipparchia aristaeus senthes* Fruhstorfer. Greece, Macedonia, near Kentrikon, 26 June (**Setae** not shown).
**Fig. 86.** *Hipparchia azorina* Strecker. Azores, Fayal, Crater lip, 1 August (**Penis** detached).
**Fig. 87.** Locality map of examined *fagi*-group taxa.
**Fig. 88.** Locality map of examined *semele*-group taxa.


PRIMARY GENITALIA
BURSA COPULATRIX
OVIDUCTUS COMMUNIS
BULLA SEMINALIS
OVIDUCTUS LATERALIS
OVARIUM
segment 2
3
4
5
6
7
8
9+10
SPERMATOTHECA
DIGESTIVE TRACT
GLANDULAE CEBACEAE
ANUS
OSTIUM OVIDUCTUS
DUCTUS SEMINALIS
VAGINA
STERIGMA
OSTIUM BURSAE
DUCTUS BURSAE
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SIGNA
CORPUS BURSAE
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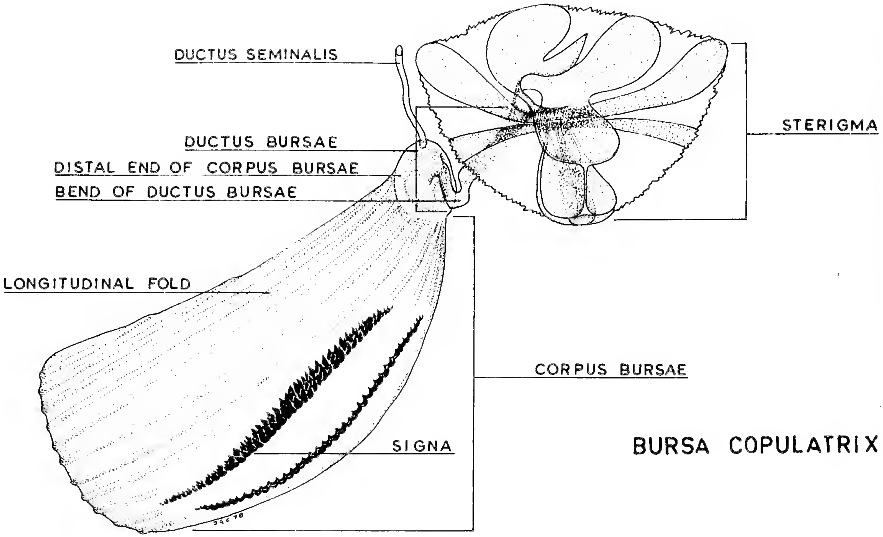
DUCTUS SEMINALIS
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DUCTUS BURSAE
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CORPUS BURSAE
SIGNA
BURSA COPULATRIX

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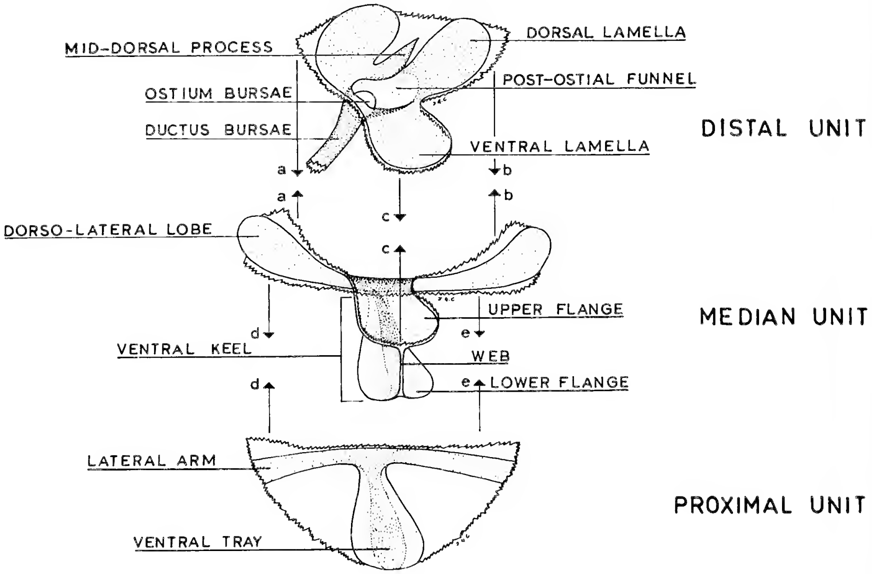
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DISTAL UNIT
VENTRAL LAMELLA
a
b
a
b
c
DORSO-LATERAL LOBE
c
UPPER FLANGE
MEDIAN UNIT
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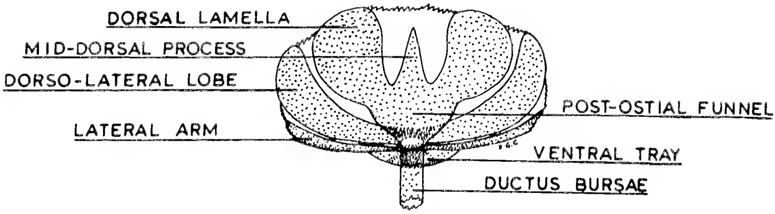
LOWER FLANGE
LATERAL ARM
PROXIMAL UNIT
VENTRAL TRAY

3


DORSAL LAMELLA
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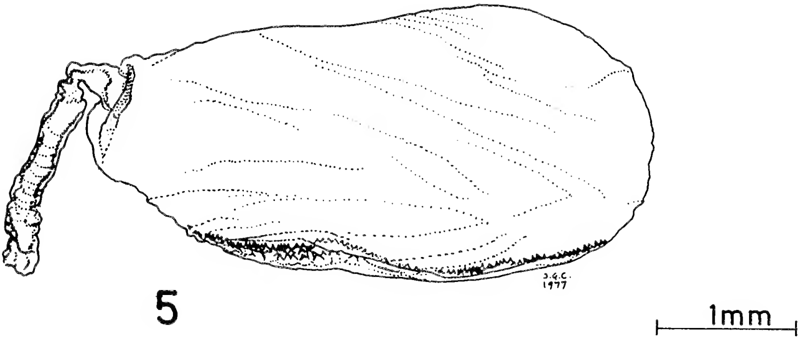
DUCTUS BURSAE
J.G.C.

4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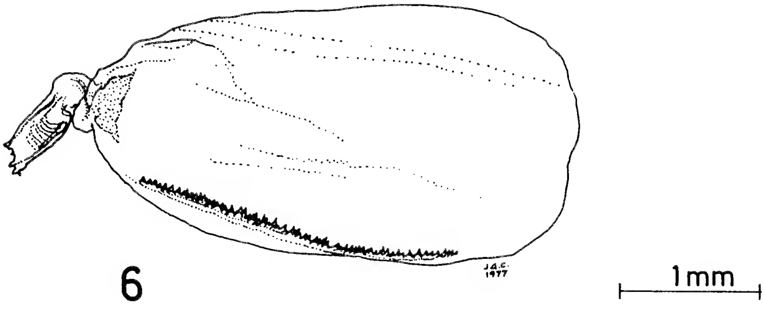
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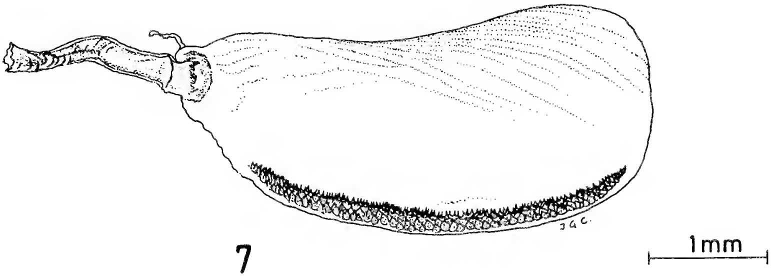

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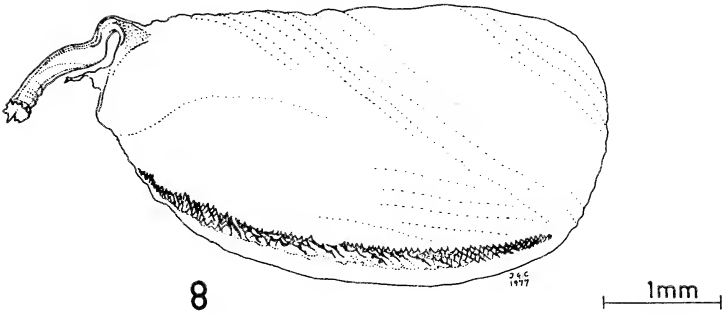

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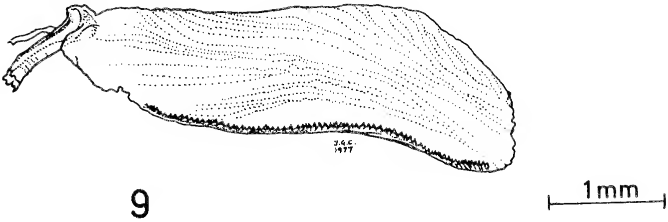

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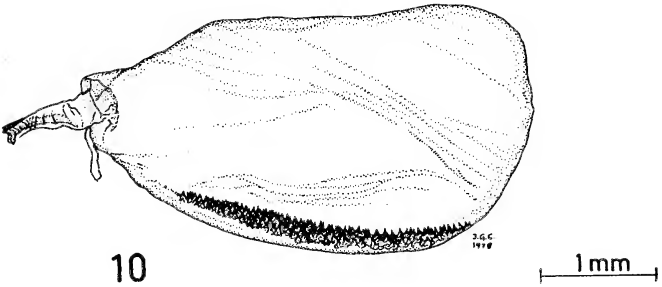

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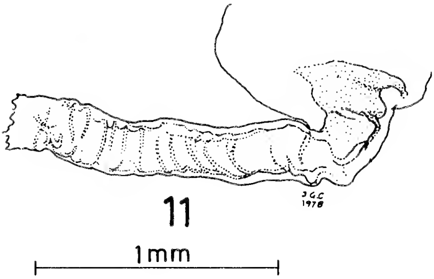

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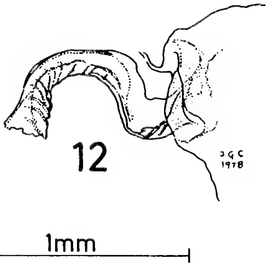

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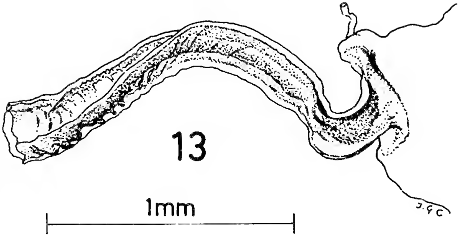

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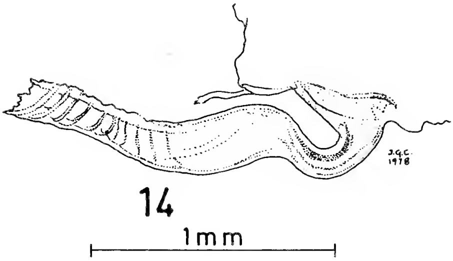

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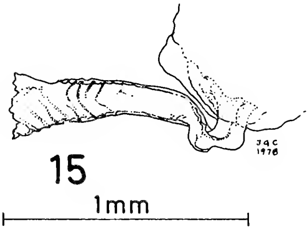

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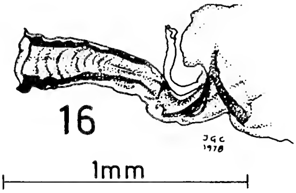

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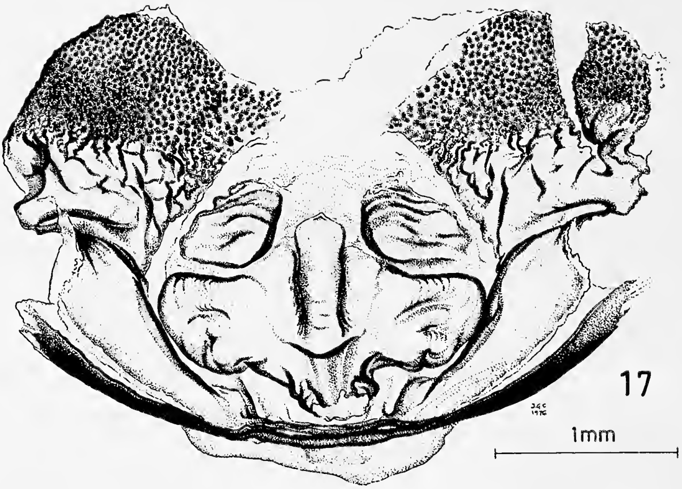

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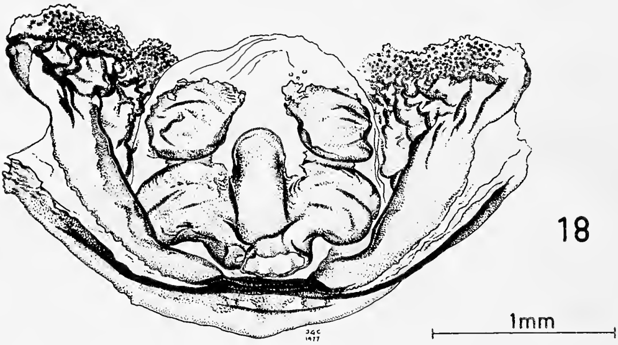

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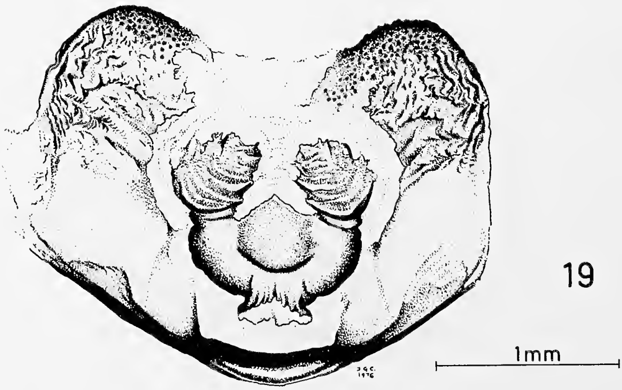

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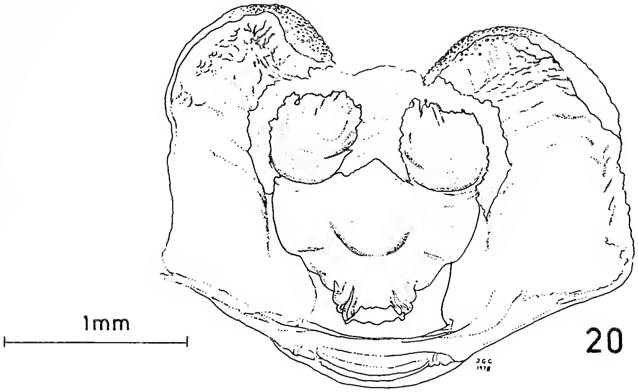

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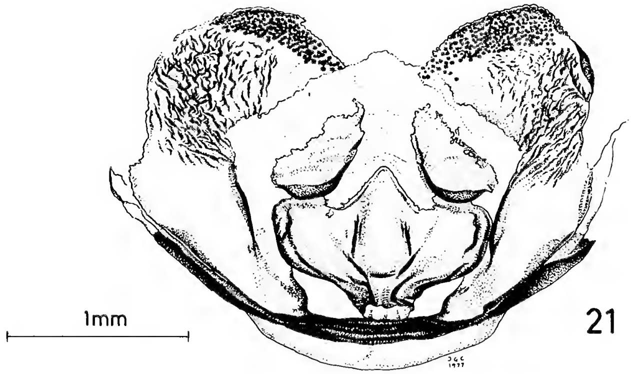

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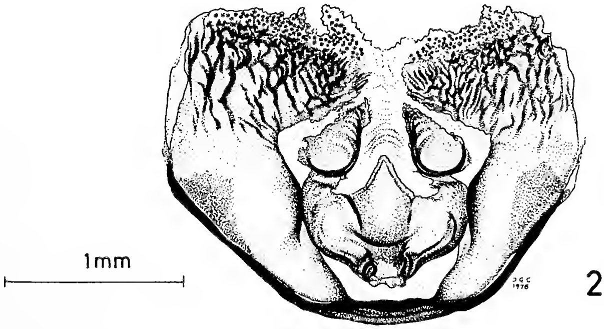

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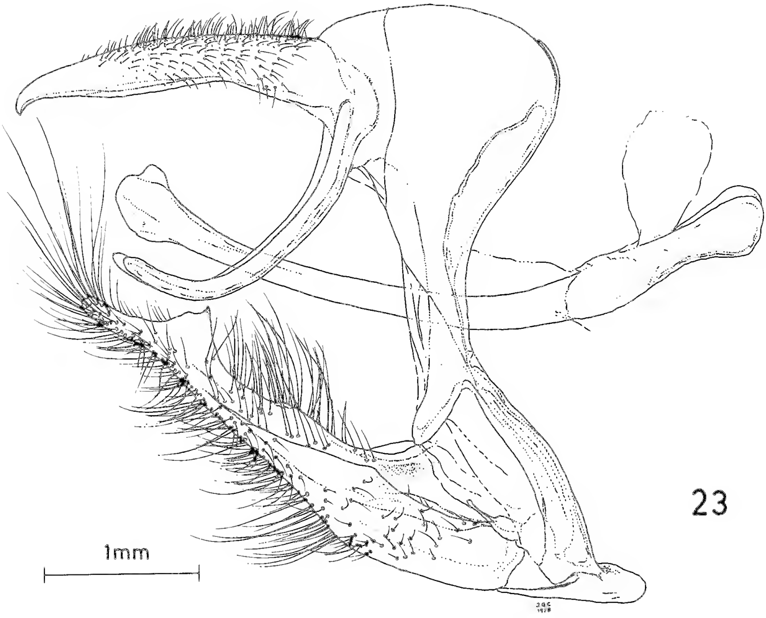

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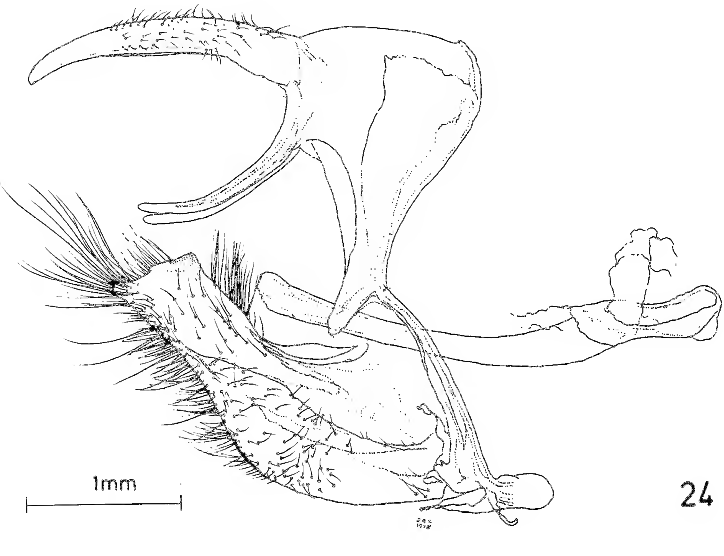

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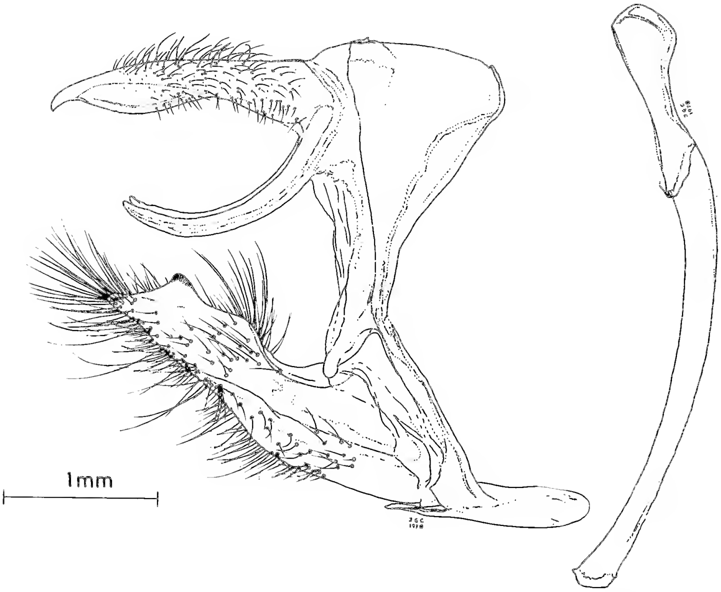

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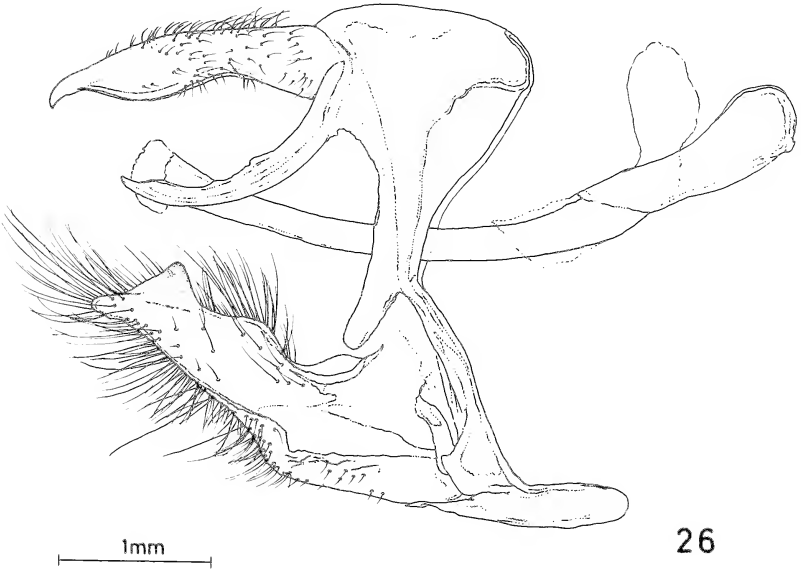

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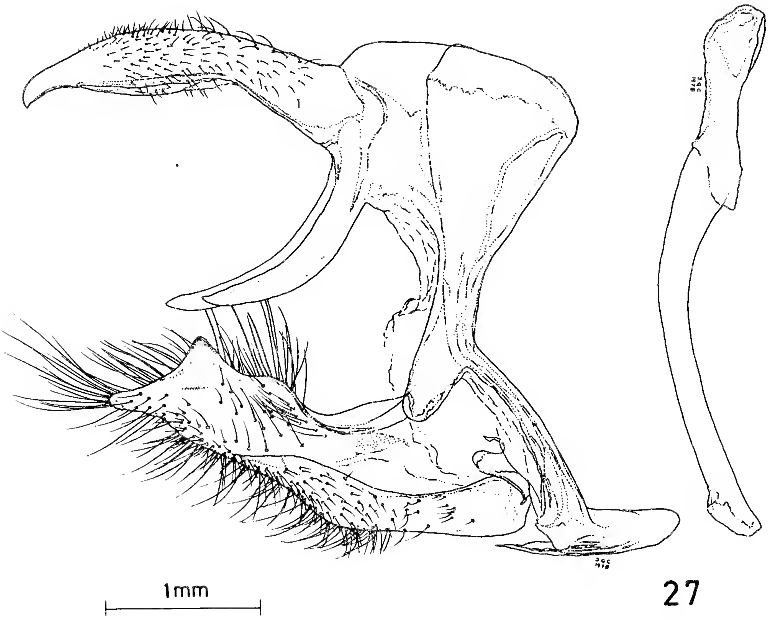

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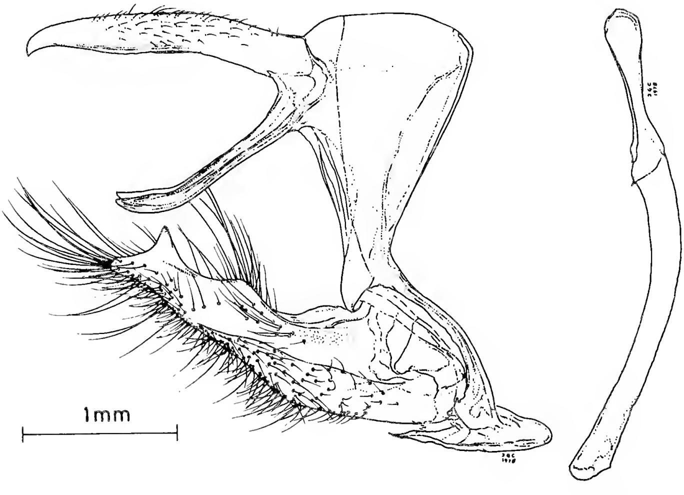

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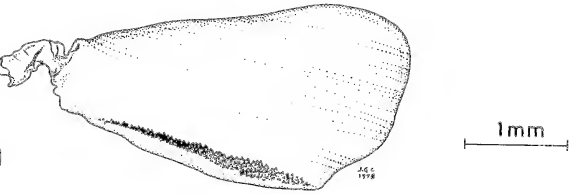

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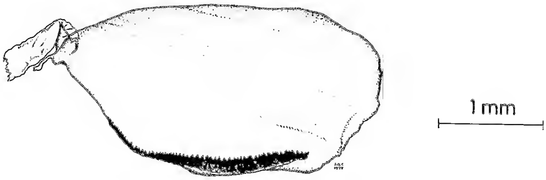

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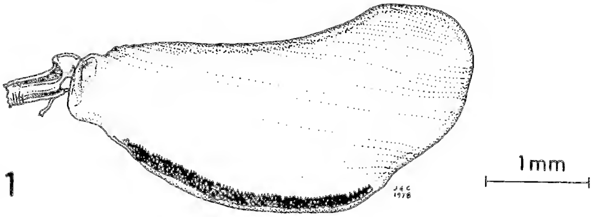

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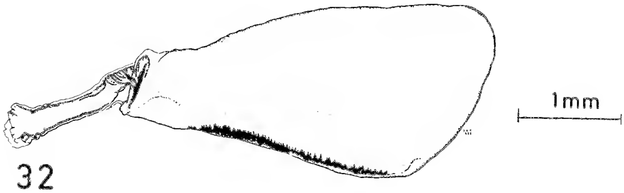

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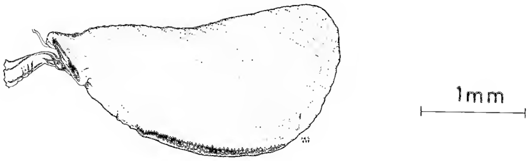

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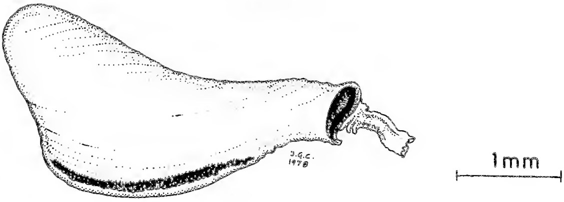

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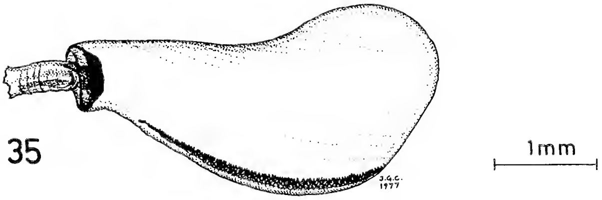

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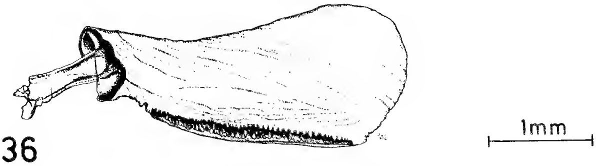

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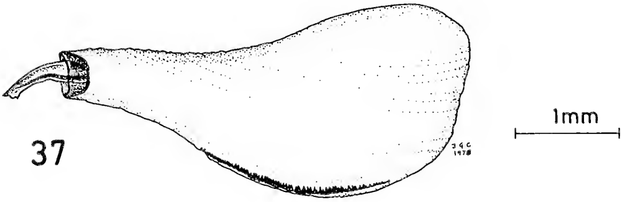

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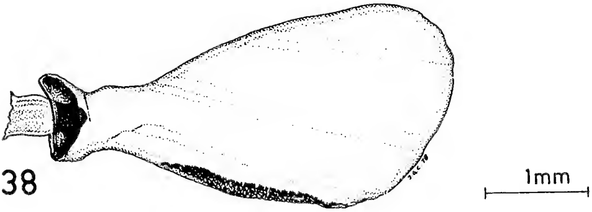

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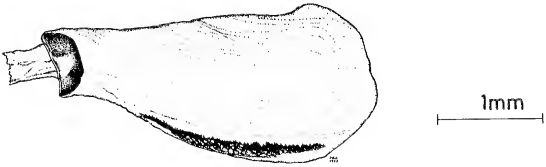

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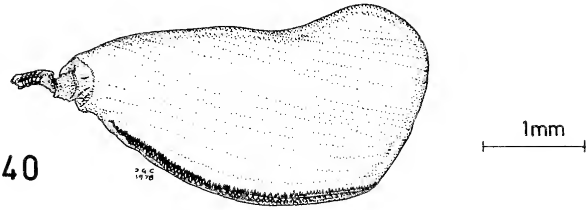

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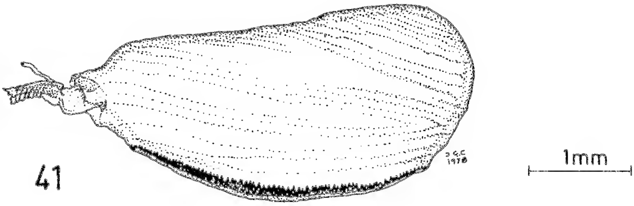

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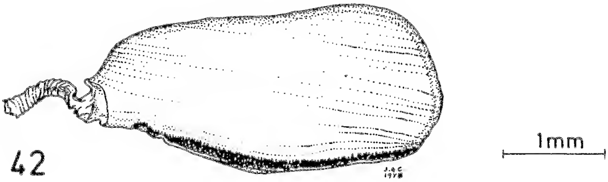

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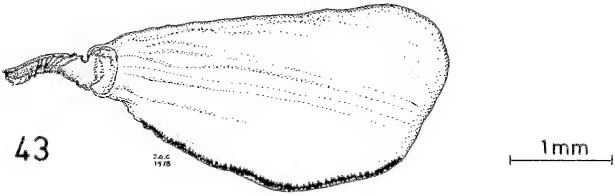

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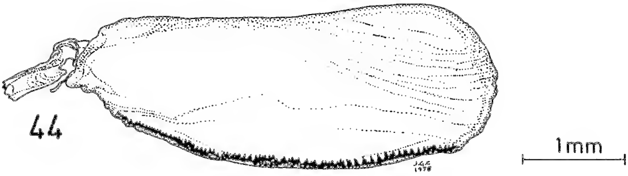

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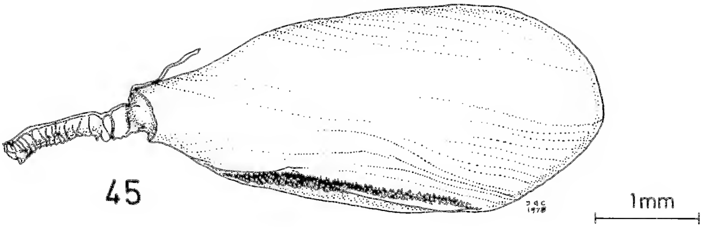

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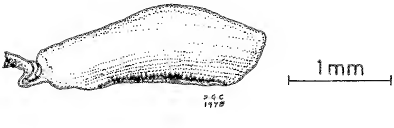

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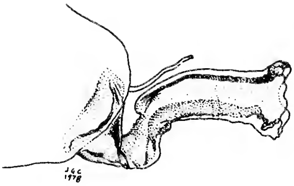

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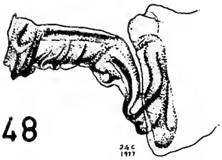

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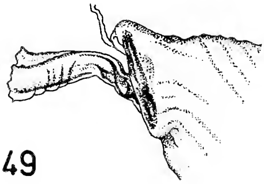

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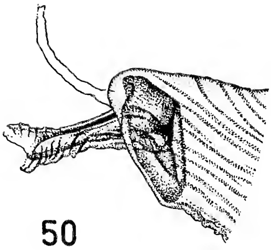

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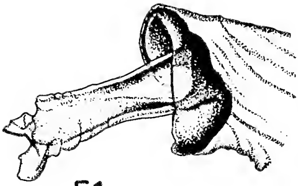

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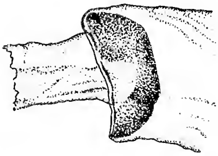

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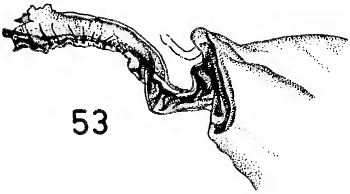

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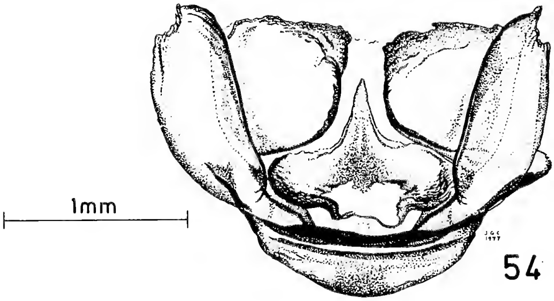

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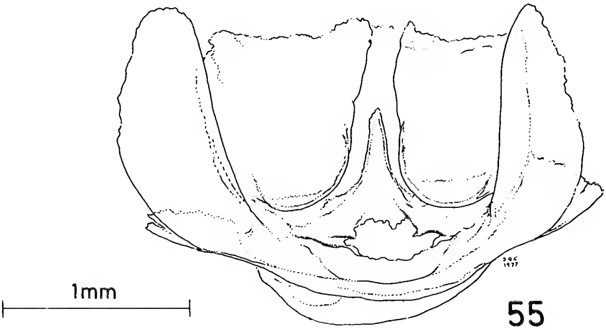

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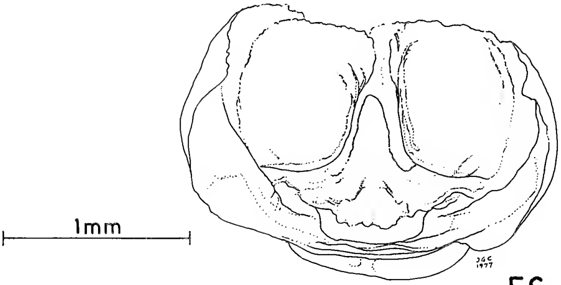

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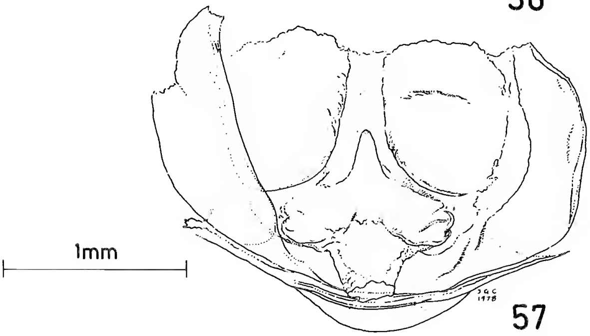

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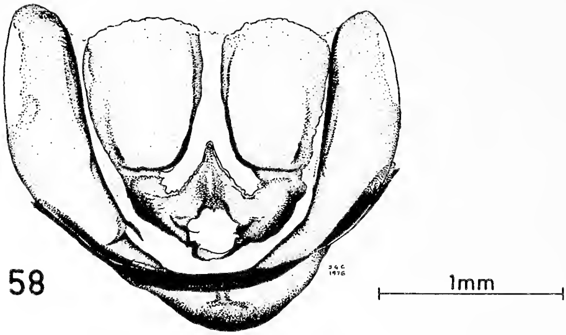

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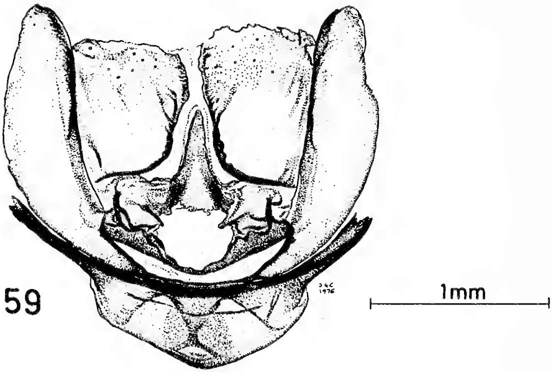

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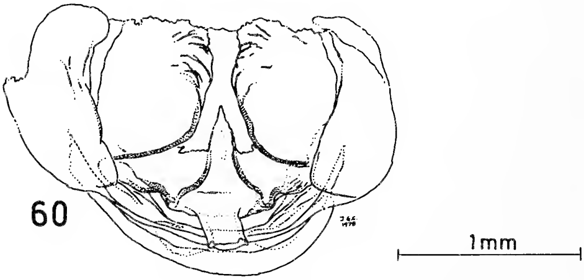

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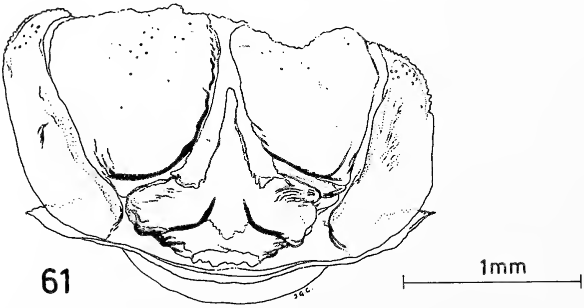

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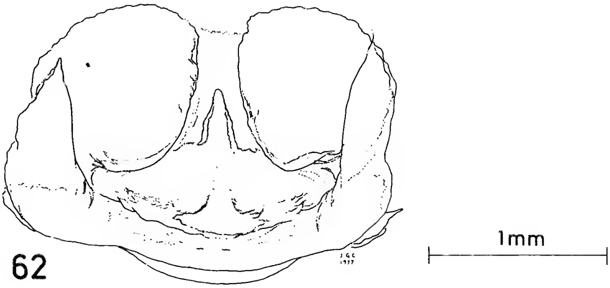

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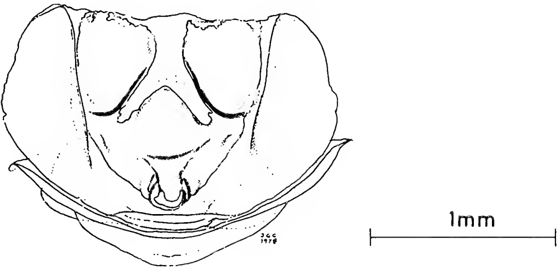

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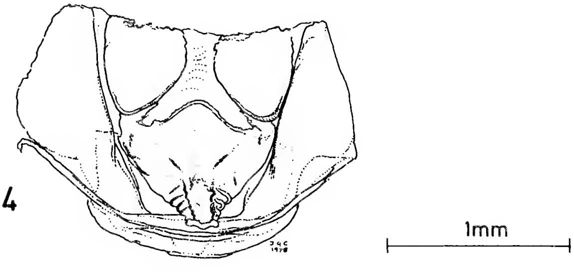

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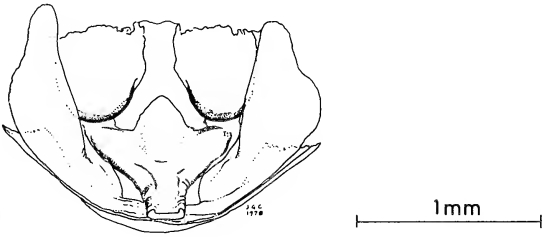

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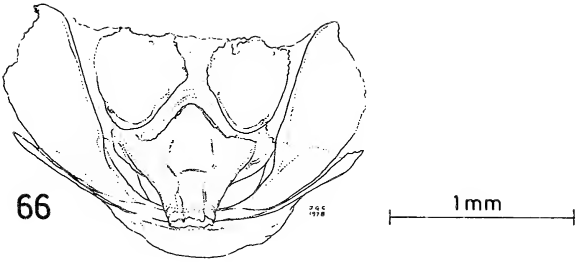

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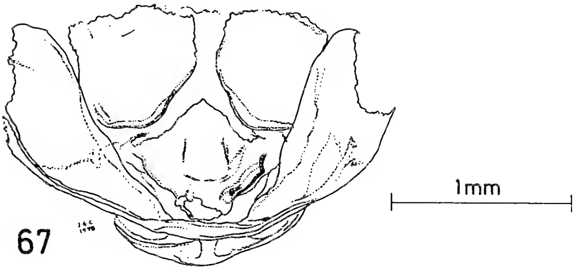

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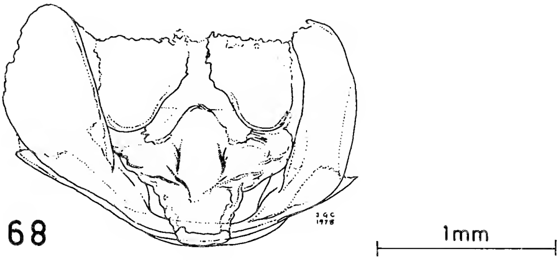

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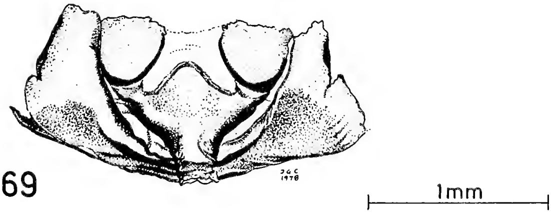

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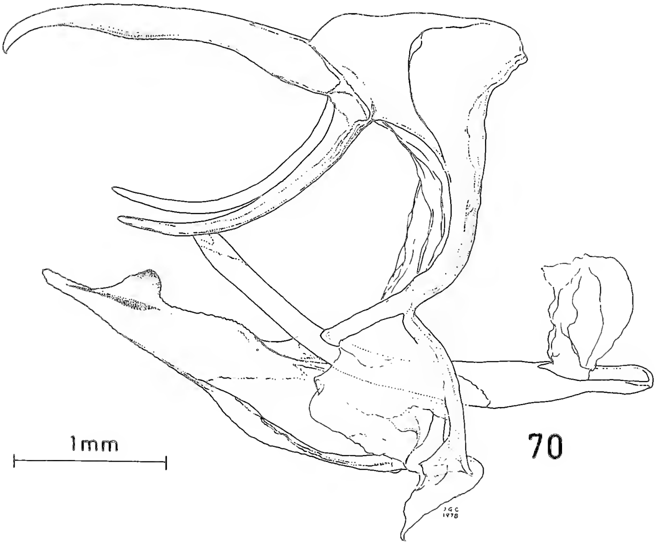

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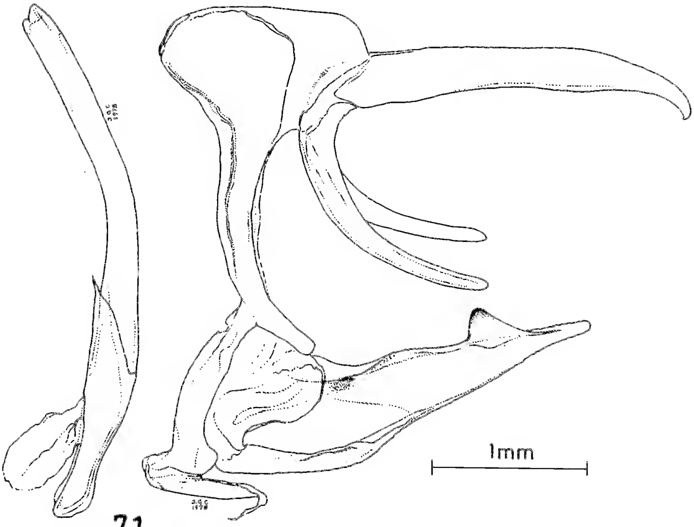

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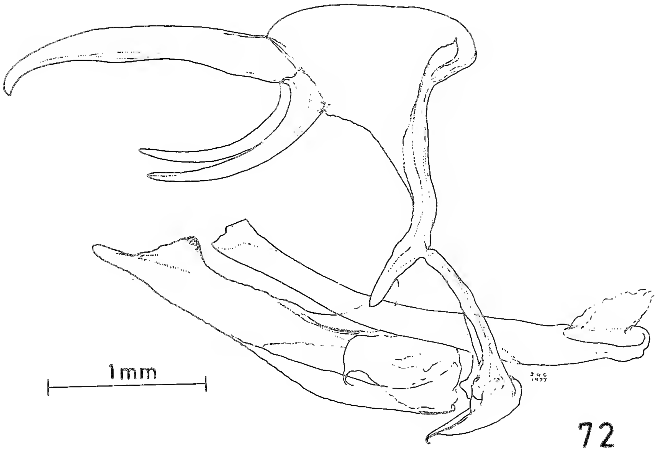

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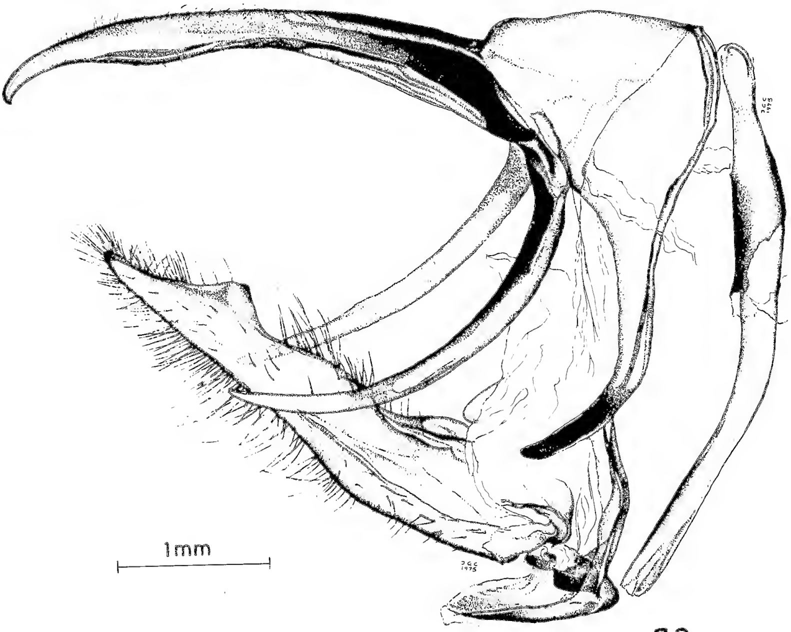

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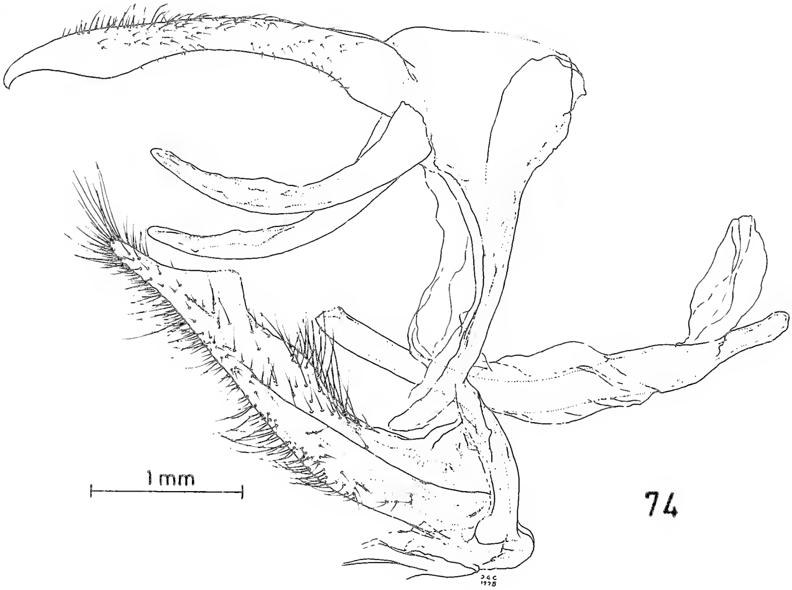

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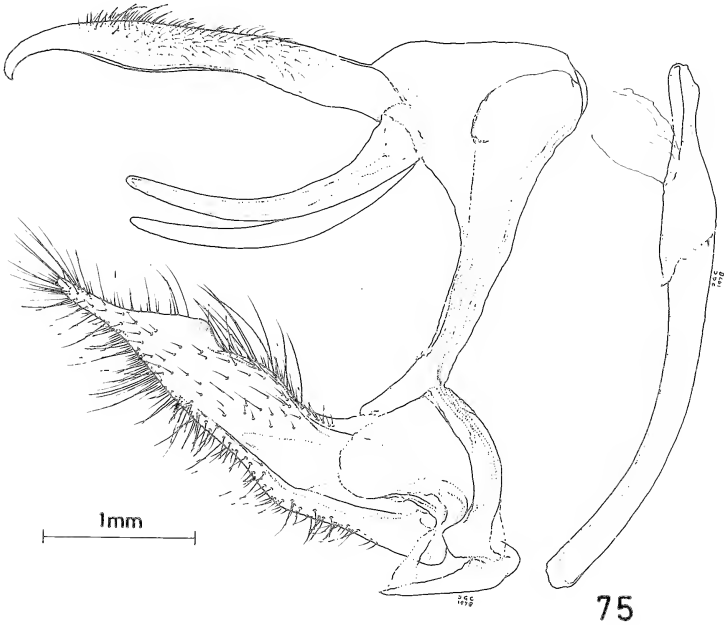

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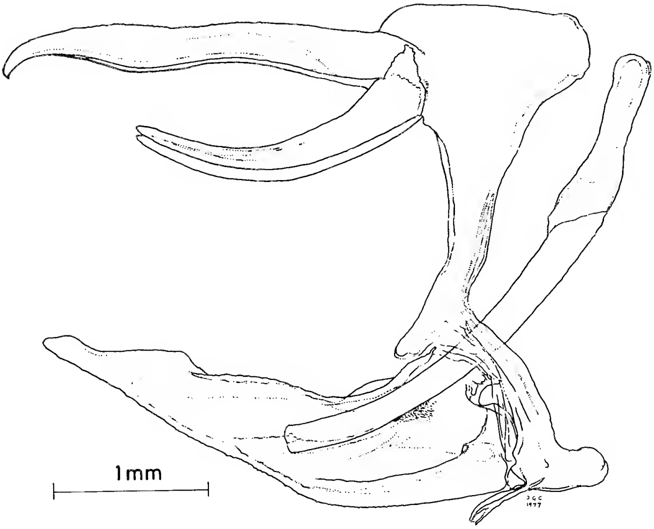

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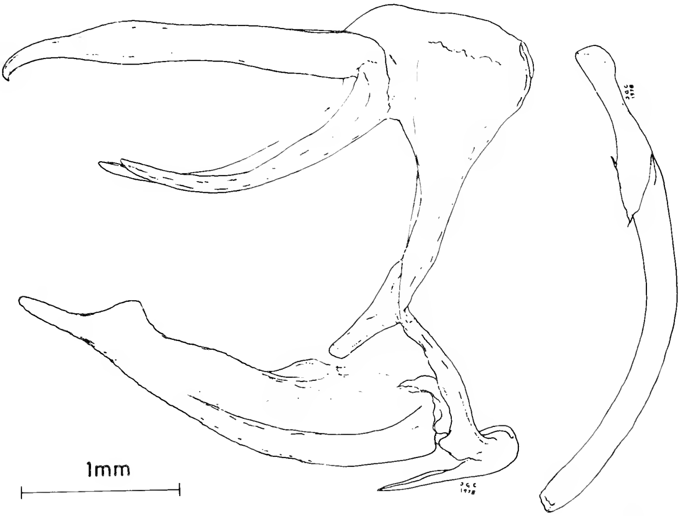

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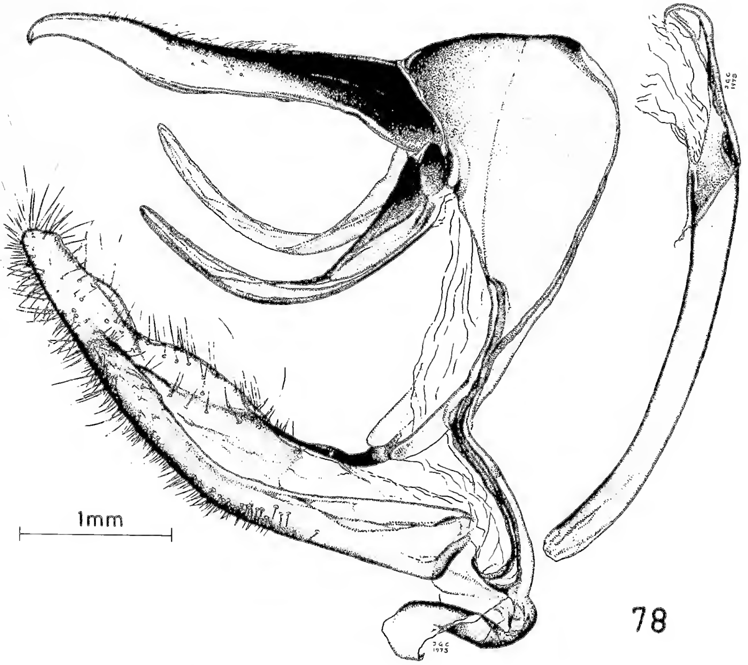

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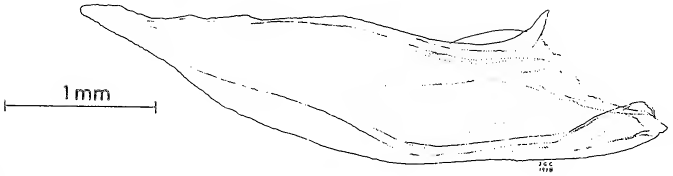

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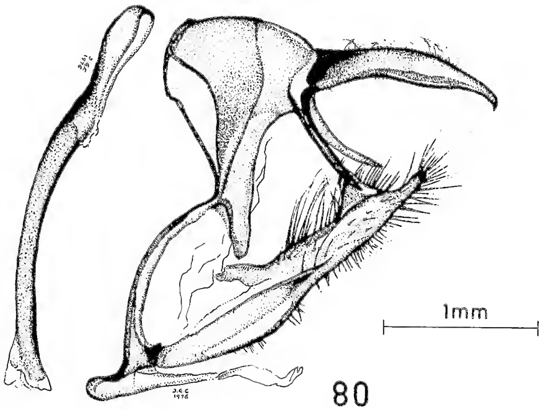

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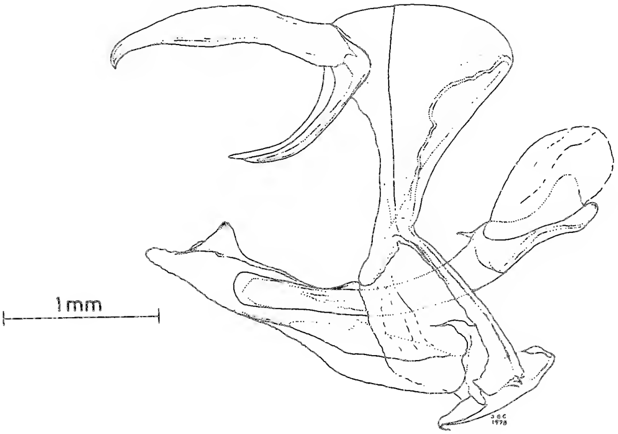

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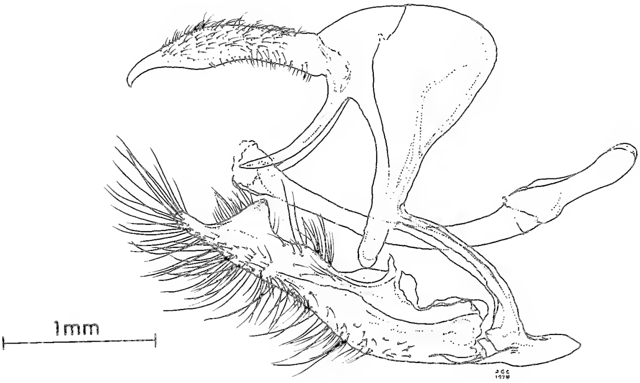

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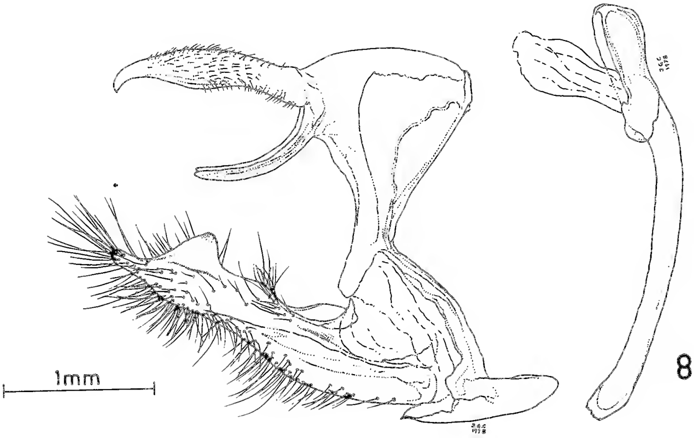

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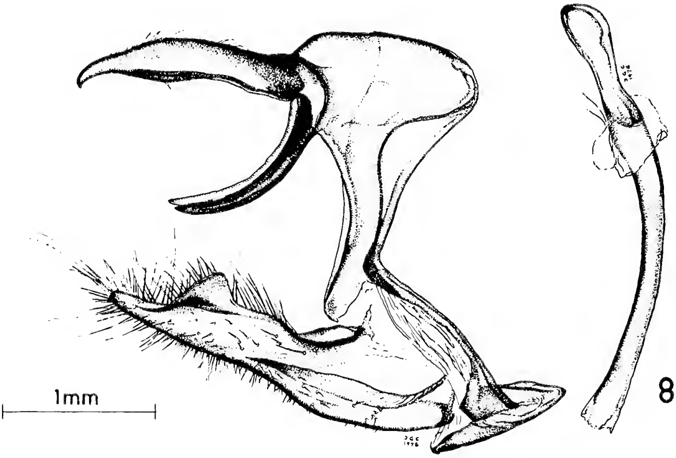

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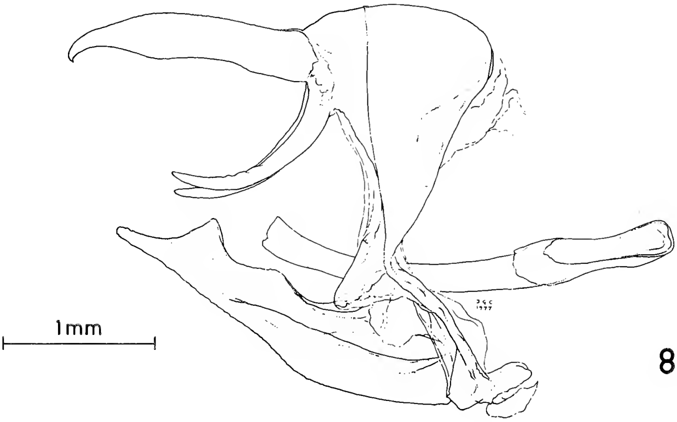

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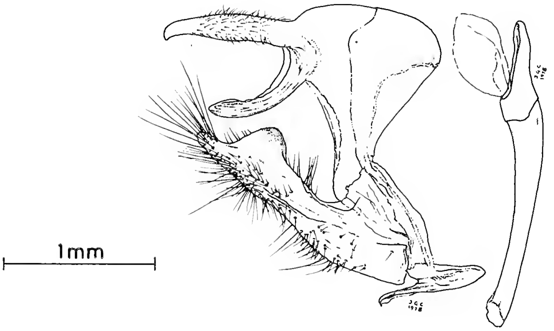

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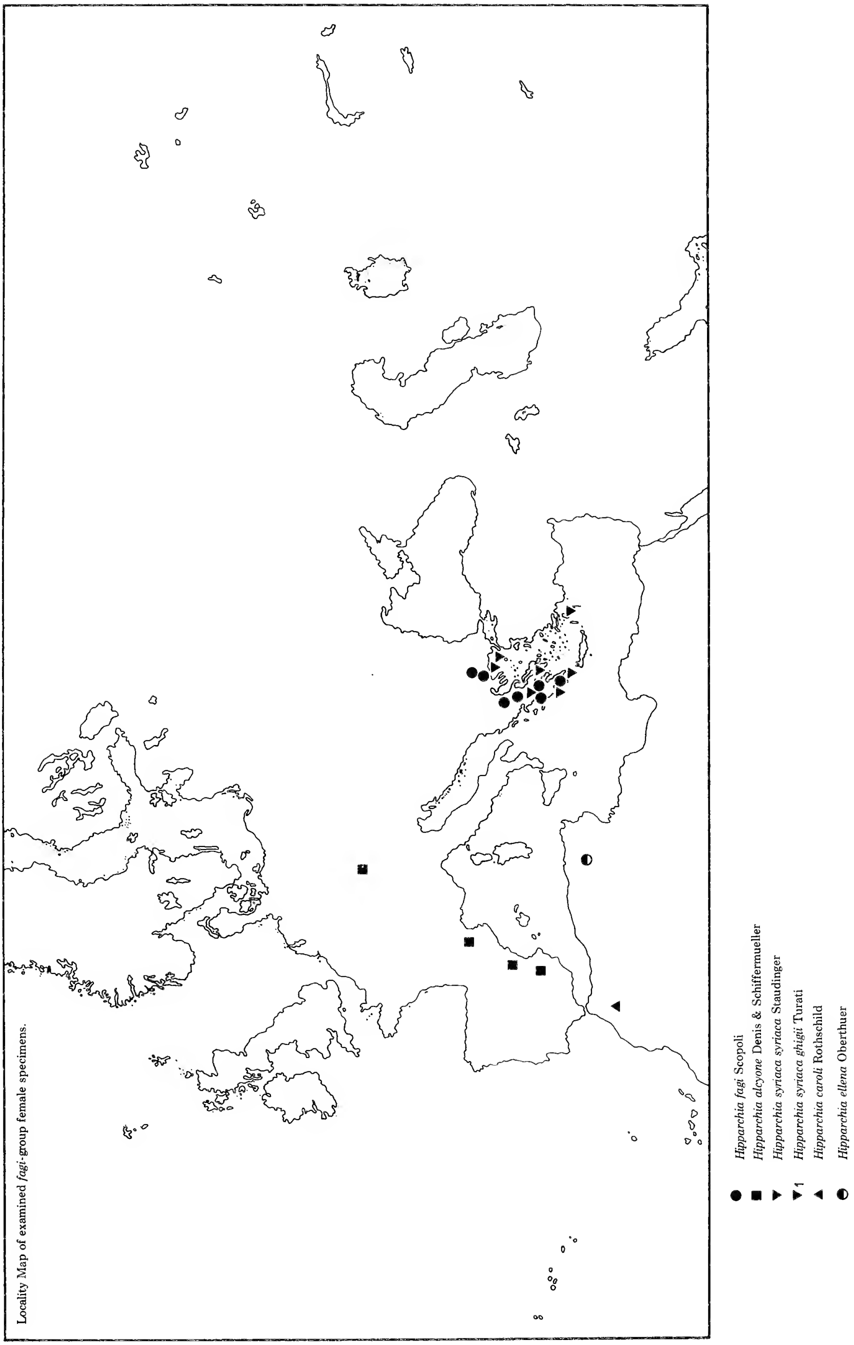
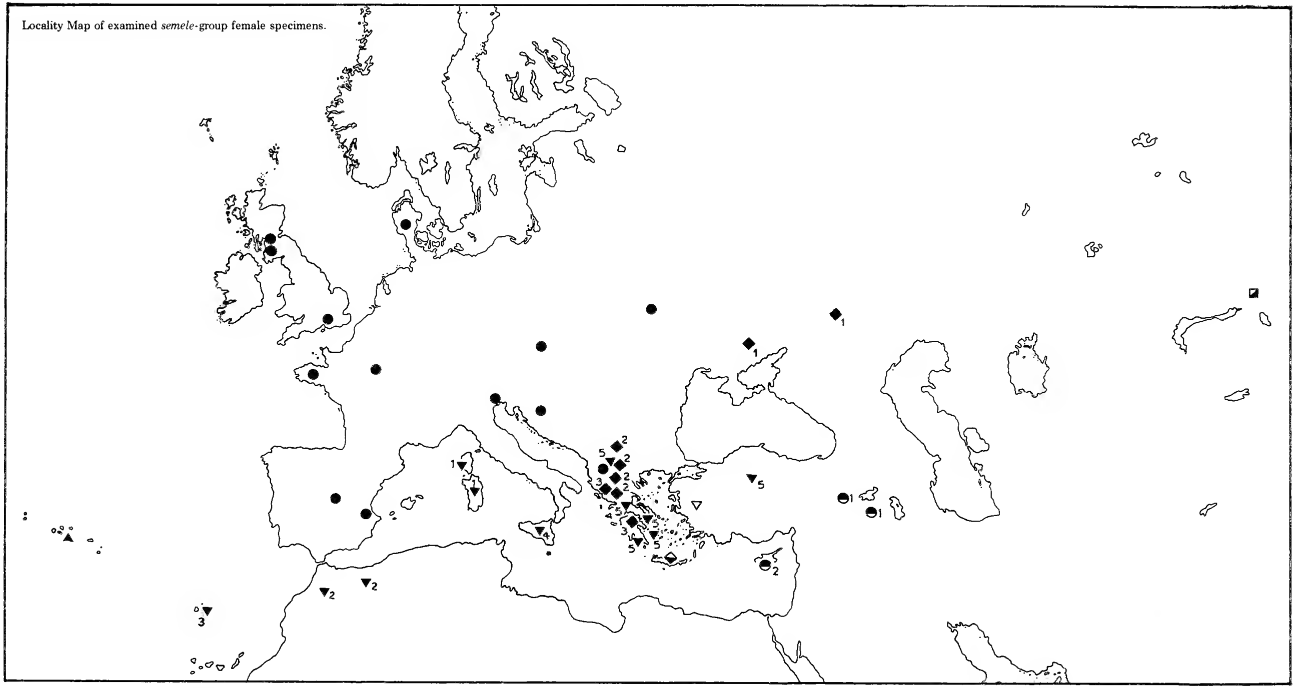


Locality Map of examined *fagi*-group female specimens.



Locality Map of examined *semele*-group female specimens.

| | |
|---|---|
| ● | *Hipparchia semele* Linnaeus |
| ⬘ | *Hipparchia cretica* Rebel |
| ▽ | *Hipparchia mersina* Staudinger |
| ◆1 | *Hipparchia volgensis volgensis* Mazochin-Porshnjakov |
| ◆2 | *Hipparchia volgensis delattini* Kudrna |
| ◆3 | *Hipparchia volgensis muelleri* Kudrna |
| ◪ | *Hipparchia turcmenica* Heydemann |
| ◒1 | *Hipparchia pellucida pellucida* Stauder |
| ◒2 | *Hipparchia pellucida cypriensis* Holik |
| ▼1 | *Hipparchia aristaeus aristaeus* Bonelli |
| ▼2 | *Hipparchia aristaeus algirica* Oberthuer |
| ▼3 | *Hipparchia aristaeus maderensis* Bethune-Baker |
| ▼4 | *Hipparchia aristaeus blachieri* Fruhstorfer |
| ▼5 | *Hipparchia aristaeus senthes* Fruhstorfer |
| ▲ | *Hipparchia azorina* Strecker |

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# Allozyme Variation in a Colonizing Species: The Cabbage Butterfly *Pieris rapae* (Pieridae)

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and

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**Abstract.** Geographic patterns of variation at 7 allozyme loci in the butterfly *Pieris rapae* agree well with those expected from a knowledge of the open population structure of the insect. In the eastern United States, where the species has existed for a longer time and where there is probably more gene flow among populations, *P. rapae* populations show little or no genetic divergence. The results of this study and of our study of population structure indicate that effective population sizes are large and that the population of the entire eastern seaboard may even approach a single, panmictic unit. In the West, areas of suitable habitat in residential or agricultural areas are separated by extensive, inhospitable areas. Populations there have apparently diverged, at least slightly, from those in the East and among themselves. Although the action of other factors, especially selection, cannot be completely ruled out, it is likely that extensive gene flow among populations is the most important force in determining the overwhelming pattern of allozyme uniformity in *P. rapae*.

## Introduction

The theory relating gene frequencies to elements of population structure (*sensu* Ehrlich, Holm and Parnell, 1974) such as the size and dynamics of populations is sophisticated and constantly growing more so. Although many aspects of this theory have been explored experimentally in laboratory populations, especially of *Drosophila*, there are few data from natural populations. Among numerous recent studies using allozyme methods to investigate genic variation in natural populations (see Lewontin, 1974; Powell, 1975; Nevo, 1978; and Hamrick *et al.*, 1979; for recent reviews), only a few have included an appreciable ecological compenent or have dealt with populations whose structure had been previously well characterized (McKechnie, Ehrlich and White, 1975; Schrier *et al.*, 1977; Hedgecock, 1978; Eanes and Koehn, 1979); yet these are the kinds of investigations that must be carried out if we seek correlation between elements of population structure and patterns of genetic variation.

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Allozyme methods reveal only a portion of the true allelic variation at structural loci. Nonetheless, if a number of loci are studied and if some care is taken to affirm the underlying genetic basis of the observed variation in electromorphs (*i.e.* protein variants of a single locus with different electrophoretic mobilities), these methods can provide more information on patterns of geneic variation than can most classical methods.

In this paper we report a study of allozyme variation in North American populations of the European Cabbage Butterfly, *Pieris rapae* (Linnaeus). An intensive study of adult population ecology accompanied the genetic investigations, and the results of that study will be reported in detail elsewhere. These studies were intended to provide quantitative data on population geometry, density and dispersal as well as on patterns of allozyme variation.

## The Organism

Butterflies have long been important subjects in ecological genetics (Ford, 1971; Ehrlich *et al.*, 1975). Although our knowledge of the ecology of butterfly populations is more advanced than our knowledge of their genetics, there is a body of data on the interaction of population structure and genetic variation (based on phenetic characters) going back to the early work of E. B. Ford and others (Ford and Ford, 1930; Ford, 1971). The use of allozyme methods promises to improve our understanding of the genetics of butterfly populations and to allow a more satisfying synthesis than previously possible (Ehrlich *et al.*, 1975; Ehrlich and White, 1980).

*Pieris rapae*, known in Britain as the small garden white and in North America as the European cabbage butterfly, can aptly be labeled a "colonizing species." Its colonizing ability is perhaps best illustrated by the history of the species' rapid spread following its introduction to North America. It was introduced in Quebec around 1860 (Scudder, 1887) and had spread as far as the California coast by the 1920's (Comstock, 1927), although it may have arrived there by a much earlier, separate introduction (Emmel and Emmel, 1973). Emmel (1975) reports that *P. rapae* spread throughout Australia in the five years following its introduction to that continent in Victoria in 1939.

The larvae feed on crucifers and can be serious pests on crop plants of that family. Within its range, *P. rapae* is ubiquitous in gardens and other areas containing wild or cultivated Cruciferae. It also inhabits other temporally unstable habitats in very early stages of secondary succession or those subject to persistent disturbance.

Our mark-recapture studies of the adult population ecology of *P. rapae* in central New York State (Vawter, in prep.) demonstrated that individuals readily move up to several kilometers between areas of suitable habitat,

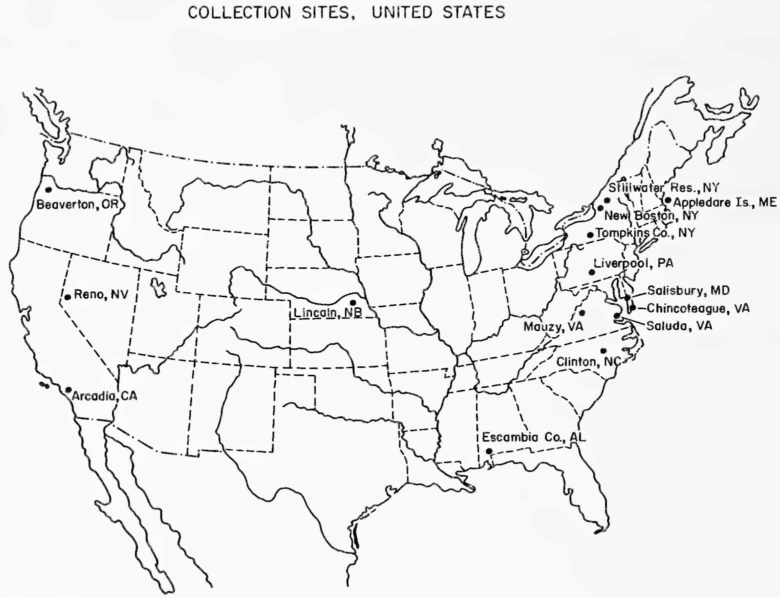

Fig. 1. Collection Sites, United States.

and that areas of concentration exchange individuals frequently. Various indices of vagility indicated that females have more of a tendency to disperse than males, and since virtually every female is inseminated shortly after emergence from the pupa, such dispersal almost certainly represents gene flow. At least some European populations of *P. rapae* are migratory.

## Methods

Collections for this study were made between 1973 and 1976 in the areas shown in Figures 1 and 2. Most of the collecting sites were agricultural fields either currently under cultivation or in various stages of secondary succession. Three of the Tompkins Co., N.Y., sites (White Church, Belle School and Caroline Depot) lie in the Willseyville Valley, in which we carried out an intensive mark-recapture program to study the adult population structure of *P. rapae*.

All sampling was done by netting. Captured specimens were placed live in glassine envelopes and either returned immediately to the laboratory (Tompkins Co. samples) or frozen and kept on dry ice. Electrophoretic techniques were similar to those used by Selander *et al.* (1971), modified for Lepidoptera as in Vawter and Brussard (1975). We originally surveyed 24 genetic loci; most were monomorphic or only weakly polymorphic. Thus, this analysis concentrates on four highly polymorphic ones (GOT-1,

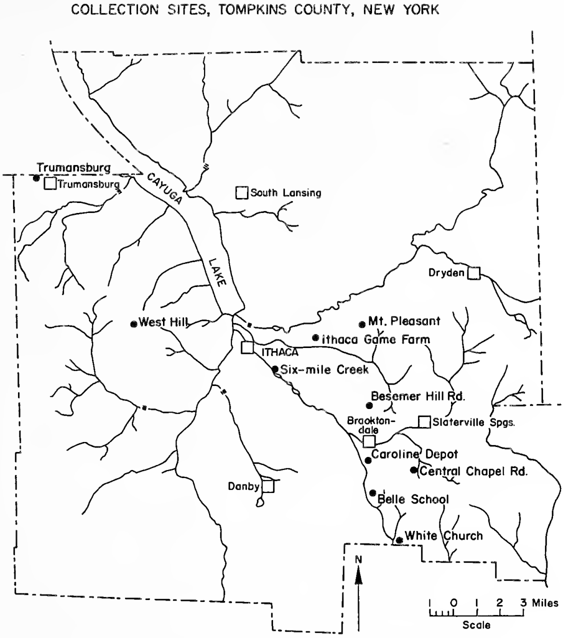

Fig. 2. Collection Sites, Tompkins County, New York.

PHI, PGM and MDH-1), and on three other slightly polymorphic loci which were clearly resolved on the same gels (MDH-2, GOT-2 and $\alpha$-GPDH).

Allelic frequencies were derived directly from the observed zygotic frequencies. After lumping some electrophoretic classes to achieve appropriately large expected frequencies, these were compared to those expected under Hardy-Weinberg equilibrium. Out of 55 possible comparisons, only one sample deviated significantly from Hardy-Weinberg expectation. In order further to confirm the genetic basis for the phenotypes observed on our gels, we carried out a laboratory breeding study as well. In no case did we discover a phenotype in the $F_1$ which could not be explained by the observed parental phenotypes; furthermore in only one case out of 45 were the observed ratios significantly different from those expected for Mendelian inheritance of single-locus characters. These results, plus the concordance of the observed electrophoretic patterns at these loci to those known in other organisms, provide convincing evidence of the underlying genetic basis of polymorphisms. No significant differences in electromorph frequencies were ever observed between sexes, and males and females were considered together for further analysis.

## Results

In cases where migration between neighboring demes is restricted, genetic differentiation on a local scale can be substantial. Although one might not, on first consideration, expect to find such patterns in populations of butterflies or other organisms capable of rapid dispersal by flight, the population structures that have been described for a number of butterfly species suggest the possibility of genetic differentiation among demes on a highly local scale (Ehrlich, 1965; Ford, 1971; Ehrlich and Gilbert, 1973; Ehrlich and Raven, 1969). To date, however, studies of genetic variation among local populations of butterflies, even those known to exchange very few individuals, have failed to reveal significant microgeographic differentiation either in phenetic (Ehrlich and Mason, 1966; Ehrlich *et al.*, 1975) or electrophoretic characters (Burns and Johnson, 1971; Ehrlich *et al.*, 1975; McKechnie *et al.*, 1975; Brussard and Vawter, 1975; Vawter and Brussard, 1975; Schrier *et al.*, 1976).

## Variation on a Local Scale

We found little evidence for microgeographic differentiation at allozyme loci among the 10 areas we sampled in Tompkins Co., N.Y., between 1973 and 1976 (Tables 1 and 2). The slightly polymorphic loci were fixed or nearly fixed for the same electromorph, and frequencies at the four polymorphic loci were similar in all populations. G-tests for heterogeneity revealed no significant variation in allelic frequencies among the three broods of *P. rapae* flying in Tompkins Co. during 1974 at GOT-1, PHI and PGM, nor at the slightly polymorphic loci. At the MDH-1 locus, however, a significant heterogeneity was detected, due to a high frequency of the MDH-1a electromorph in Brood 1. This difference disappeared in

Table 1. Frequency of most common electromorph at localities within Tompkins Co., NY, 1973-1976

| Locality & Date | Sample Size | GOT-1a | GOT-2b | PHIc | PGMb | $\alpha$GPDH$\alpha$ | MDH-1b | MDH-2b |
|---|---|---|---|---|---|---|---|---|
| Wilseyville Valley 1973 | | | | | | | | |
| White Church | 114 | 0.87 | 1.00 | 0.78 | 0.72 | 0.95 | 0.91 | 0.98 |
| Belle School | 107 | 0.86 | 0.99 | 0.71 | 0.69 | 1.00 | 0.93 | 0.99 |
| Trumansburg 1973 | 27 | 0.85 | — | 0.74 | 0.70 | — | 0.96 | 1.00 |
| Ithaca Game Farm 1973 | 32 | 0.84 | — | 0.68 | 0.75 | 1.00 | 0.93 | 0.97 |
| Besemer Hill Rd. 1973 | 50 | 0.87 | 1.00 | 0.73 | 0.77 | 1.00 | 0.90 | 0.98 |
| Wilseyville Valley 1974 | 266 | 0.83 | 0.99 | 0.74 | 0.74 | 1.00 | 0.92 | 0.90 |
| Central Chapel Rd. 1974 | 34 | 0.88 | 0.98 | 0.68 | 0.74 | 1.00 | 0.90 | 1.00 |
| Six-mile Creek 1974 | 24 | 0.94 | 0.98 | 0.88 | 0.90 | 1.00 | 0.87 | 1.00 |
| West Hill 1974 | 21 | 0.90 | 0.96 | 0.76 | 0.75 | 1.00 | 1.00 | — |
| Wilseyville Valley 1975 | 46 | 0.89 | 1.00 | 0.80 | 0.75 | 1.00 | 0.88 | 1.00 |
| Mt. Pleasant 1976 | 50 | 0.87 | 1.00 | 0.69 | 0.64 | 1.00 | 0.94 | 0.98 |

Table 2. Heterogeneity of allozyme frequencies among localities in Tompkins Co., NY. The localities sampled each year are listed below.

| | G | df | P |
|---|---|---|---|
| **1973**[1] | | | |
| GOT-1 | 2.78 | 8 | >0.9 |
| PHI | 15.73 | 16 | >0.1 |
| PGM | 17.14 | 16 | >0.1 |
| MDH-1 | 2.78 | 4 | >0.5 |
| **1974**[2] | | | |
| GOT-1 | 9.50 ( 5.17) | 4 (3) | >0.025 (>0.1) |
| PHI | 23.08 (13.50) | 12 (9) | >0.025 (>0.1) |
| PGM | 19.84 | 16 | >0.1 |
| MDH-1 | 3.02 | 4 | >0.5 |
| **1973, 1974, 1976**[3] | | | |
| GOT-1 | 7.07 | 7 | >0.1 |
| PHI | 31.63 | 21 | >0.05 |
| PGM | 34.08 | 28 | >0.1 |
| MDH-1 | 5.35 | 7 | >0.5 |

[1] White Church, Belle School, Besemer Hill Road, Trumansburg, Ithaca Game Farm.

[2] Belle School, Caroline Depot, Six-Mile Creek, Central Chapel Road, West Hill. Values in parentheses were calculated w/o Six-mile Creek.

[3] Trumansburg, Ithaca Game Farm, Besemer Hill Road (1973); Wilseyville Valley combined, Central Chapel Road, Six-mile Creek, West Hill (1974); Mt. Pleasant (1976).

subsequent years, however. Finally, G-tests revealed no heterogeneity among allelic frequencies at any locus among years (1973-1975) in the Willseyville Valley. Thus, samples taken anywhere within the valley were pooled for comparison with other areas. Table 2 shows the results of heterogeneity tests among Tompkins Co. localities. For 1973 we detected heterogeneities at two of the four polymorphic loci.

Examination of the 1974 electromorph frequencies themselves indicated that the Six-mile Creek population was aberrant at both GOT-1 and PHI, and perhaps at MDH-1 (Table 1), and when this population was removed from the comparison, the heterogeneity disappeared. The heterogeneity observed when the Six-mile Creek population was included, although significant at the 0.05 level, was not striking; and, given the relatively small sample size from this population (N=24), it may merely represent sampling error.

With the possible exception of Six-mile Creek, therefore, the overall pattern of genetic variation at the local level for *P. rapae* is one of genetic constancy without significant microgeographic differentiation. When we compared electromorph frequencies among all of the Tompkins Co. localities regardless of year of sampling (Table 1), we found no significant heterogeneities. That is to say, there is no genetic evidence which suggests that *P. rapae* in Tompkins Co. do not represent a single, essentially panmictic population.

## Variation on a Continental Scale

In addition to the Tompkins Co. sites, we collected allozyme data from 14 additional sites that span most of the range of *P. rapae* in North America (Table 3, Figure 1). There is a striking pattern of genetic constancy over this area as well. At the four slightly polymorphic loci, the same electromorph is fixed or nearly so in all populations, and frequencies at the polymorphic loci are similar throughout. Although populations in the western United States (Lincoln, Neb.; Beaverton, Ore.; Reno, Nev.; Arcadia, Calif.) and near the southern periphery of the species' range (Escambia Co., Ala.) show some noticeable differences, the same electromorph predominates in all populations, and the order of electromorphs from most to least common is nearly the same. The apparent fixation of the MDH-1b electromorph at Lincoln, Neb., may be a result of the small sample size in this case.

Table 3. Frequency of most common electromorph at localities outside of Tompkins Co., N.Y., various years.

| Locality | Sample Size | GOT-1a | GOT-2b | PHIc | PGMb | αGPDHa | MDH-1b | MDH-2b |
|---|---|---|---|---|---|---|---|---|
| Stillwater Reservoir, NY | 38 | 0.90 | 1.00 | 0.76 | 0.68 | 0.99 | 0.96 | — |
| New Boston, NY | 38 | 0.89 | 0.99 | 0.74 | 0.64 | 1.00 | 0.96 | — |
| Appledore Island, NH | 20 | 0.92 | 1.00 | 0.80 | 0.63 | 1.00 | 0.93 | 1.00 |
| Liverpool, PA | 28 | 0.91 | 1.00 | 0.80 | 0.70 | 1.00 | 0.90 | 1.00 |
| Salisbury, MD | 33 | 0.82 | 1.00 | 0.77 | 0.67 | 1.00 | 0.93 | 1.00 |
| Chincoteague, VA | 41 | 0.82 | 1.00 | 0.82 | 0.58 | 1.00 | 0.83 | — |
| Mauzy, VA | 44 | 0.81 | 0.99 | 0.83 | 0.74 | 1.00 | 0.91 | 1.00 |
| Saluda, VA | 72 | 0.84 | 1.00 | 0.78 | 0.70 | 1.00 | 0.90 | 0.98 |
| Clinton, NC | 29 | 0.88 | 1.00 | 0.67 | 0.68 | 1.00 | 0.93 | 1.00 |
| Escambia, AL | 46 | 0.97 | 0.99 | 0.83 | 0.82 | 1.00 | 0.91 | 0.99 |
| Lincoln, NB | 34 | 0.91 | 1.00 | 0.64 | 0.90 | — | 1.00 | 1.00 |
| Reno, NV | 92 | 0.96 | 1.00 | 0.80 | 0.68 | 1.00 | 0.92 | 1.00 |
| Beaverton, OR | 52 | 0.88 | 1.00 | 0.85 | 0.73 | 1.00 | 0.87 | 1.00 |
| Arcadia, CA | 82 | 0.88 | 1.00 | 0.84 | 0.87 | — | 0.93 | 0.99 |

The similarity among the eastern U.S. populations is well illustrated by the results of G-tests of heterogeneity (Table 4) performed on the number of genes sampled at each of the four polymorphic loci (2N). For three of the four loci (GOT-1, PHI and MDH-1), there are no significant differences among 10 localities ranging from northern New York State to central North Carolina, while for the fourth locus (PGM) the heterogeneity among these localities is significant and due primarily to the contribution of a single population (Chincoteague, Va.). The Escambia Co., Ala., population is the most aberrant of the eastern U.S. populations.

Table 4. Heterogeneity of allozyme frequencies among eastern U.S. localities. Localities include: Stillwater Reservoir, NY; New Boston, NY; Wilseyville Valley, NY (1974); Appledore Island, NH; Liverpool, PA; Salisbury, MD; Chincoteague, VA; Mauzy, VA; Saluda, VA; Clinton, NC; and Escambia Co., AL.

| | G | df | P |
|---|---|---|---|
| **Without Escambia Co., AL** | | | |
| GOT-1 | 9.76 | 9 | >0.1 |
| PHI | 26.99 | 27 | >0.1 |
| PGM | 41.27 | 27 | >0.025 |
| MDH-1 | 13.09 | 9 | >0.05 |
| **With Escambia Co., AL** | | | |
| GOT-1 | 23.62 | 10 | >0.01 |
| PHI | 31.47 | 30 | >0.1 |
| PGM | 52.88 | 30 | >0.005 |
| MDH-1 | 13.16 | 10 | >0.05 |

The western populations are not only different from the eastern populations, they also tend to be more heterogeneous among themselves. At the GOT-1 locus, an electromorph (a′) which does not occur in any eastern population occurs at very low frequency at both Lincoln, Neb., and Beaverton, Ore.; but in general, the difference between the western and eastern populations tends to be the absence in the west of electromorphs that are rare in the east.

There is, then, a striking pattern of uniformity in allozyme frequencies among populations. Eastern populations from New York to North Carolina form a homogeneous unit. However, geographically peripheral populations tend to diverge from this pattern. We made pair-wise comparisons based on all 7 loci between all populations using the index of genetic identity described by Nei (1972) for which a value of 1.00 indicates complete allelic identity (*i.e.* all alleles shared in identical frequencies). In hopes of identifying clusters of populations, we performed a Bray-Curtis ordination on two axes, using arcsine transforms of the genetic distances (see Brussard, 1975, for a description of this technique). The results of this ordination are shown in Figure 3. We chose the two genetically most dissimilar sites, Lincoln, Neb., and Chincoteague, Va., (I=.973), as the end-points of the first axis, and Six-mile Creek, N.Y., and Clinton, N.C., (I=.988) as the end-points of the second axis. Some degree of clustering

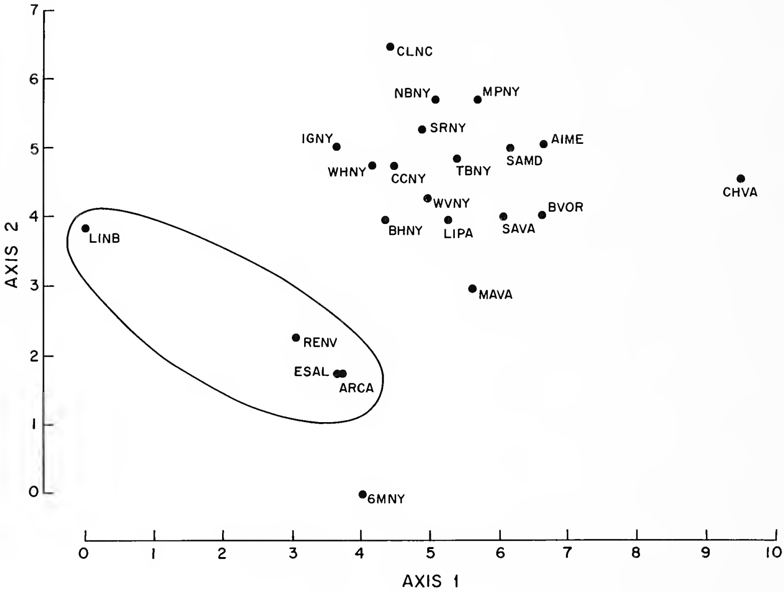

Fig. 3. 2-axis Bray-Curtis plot on arcsine transforms of genetic distance. Based on frequencies of 18 electromorphs in 22 populations. Note the tendency for geographically peripheral populations to diverge from most of the populations of the eastern United States. Beaverton, Oregon, is an exception.

AIME, Appledore Island, ME
ARCA, Arcadia, CA
BHNY, Besemer Hill, NY
BVOR, Beaverton, OR
CCNY, Central Chapel Rd., NY
CHVA, Chincoteague, VA
CLNC, Clinton, NC
ESAL, Escambia Co., AL
IGNY, Ithaca Game Farm, NY
LINB, Lincoln, NB
LIPA, Liverpool, PA
MAVA, Mauzy, VA
MPNY, Mount Pleasant, NY
NBNY, New Boston, NY
RENV, Reno, NV
SAMD, Salisbury, MD
SAVA, Saluda, VA
SRNY, Stillwater Res., NY
TBNY, Trumansburg, NY
WHNY, West Hill, NY
WVNY, Wilseyville Valley, NY
6MNY, Six-mile Creek, NY

was obtained by this analysis, indicating the central-peripheral dichotomy mentioned earlier. Two of the western populations (Reno, Nev., and Arcadia, Calif.) cluster with Escambia Co., Ala., in the lower left of the plot, but another western population (Beaverton, Ore.) is distant from these. Neither of the axes appears to parallel latitude or longitude, and geographically close sites are frequently quite distant from each other in this ordination. Another ordination based on Roger's (1972) Coefficient of Genetic Similarity without transformation, done using the Cornell Ecology Program Series (CEP-4, Gauch, 1973) produced nearly identical results, indicating that the patterns were not an artifact of the distance measure or transformation chosen. A 3-axis principal components plot based directly on the electromorph frequencies (Fig. 4) shares many similarities with the Bray-Curtis plots; the clusters are similar, and the extreme populations are the same, although Beaverton, Ore., now appears with other peripheral populations. The similarity between the aberrant Six-mile Creek sample and geographically peripheral populations is also well illustrated.

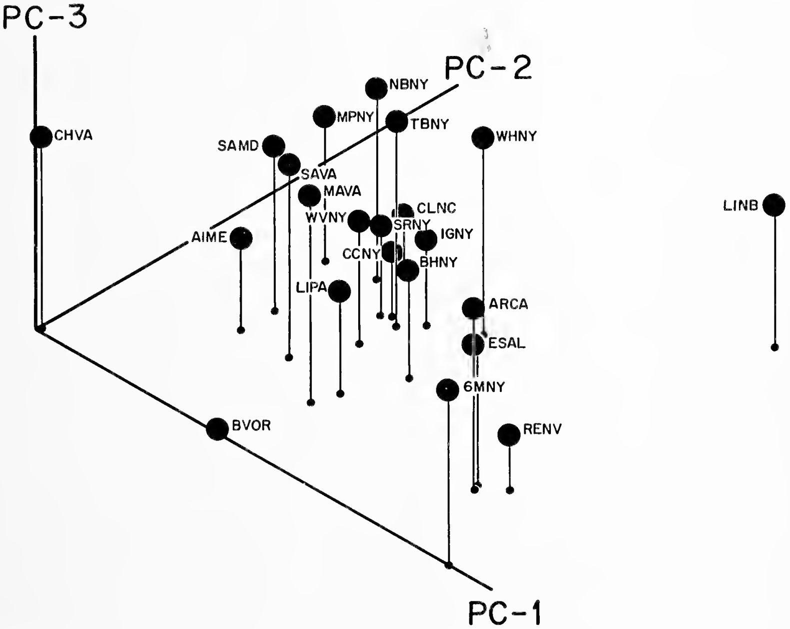

Fig. 4. 3-axis principal component plot on electromorph frequencies. Based on the same data as Figure 3. Note that geographically peripheral populations are separated from most eastern U. S. populations in this plot. Beaverton, OR, although similar to eastern U. S. populations on PC axis 1, is separated from them on axes 2 and 3. Abbreviations are the same as in Figure 3.

## Discussion

In any species that readily colonizes disturbed, temporally unstable habitats, two processes tend to work against each other to determine genetic patterns among and within populations. On the one hand, to take advantage of newly available areas for colonization, such species must be relatively vagile and have a considerable dispersal ability. From our study of the population structure of *Pieris rapae*, it appears that this species fits this requirement well, and one would expect that frequent movements among neighboring populations and occasional long-distance migration would tend to swamp any tendency toward interpopulation differentiation. On the other hand, if newly available areas are colonized by a small number of founders and if population size tends to fluctuate drastically, as one might expect it to do in temporally unstable habitats, one would expect to find a considerable degree of genetic variation among populations. Within such populations, many of which must be marginal in an ecological sense, low effective population size, founder effects, and inbreeding should also tend to reduce within-population variation (Soulé, 1973). Geographic patterns of allozyme variation in *P. rapae* reflect the action of both of these processes operating at different intensities in different parts of the species' North American range.

In a study of variation at 11 allozyme loci in the checkerspot butterfly, *Chlosyne palla* Boisduval, Schrier *et al.* (1976) found no significant differences in gene frequencies among areas separated by up to 12 km. In the same study, these authors demonstrated an "open" structure for populations of *C. palla*, and suggest that this pattern of movement and the resultant geographic uniformity of allozyme frequencies was correlated with foodplant distribution. The foodplants of *P. rapae* are very widespread; they are also largely ephemeral. This fact may account for the population structure observed in this colonizing species and the lack of significant genic difference among populations separated by thousands of km. Frequent population extinction and recolonization in weedy or otherwise ephemeral habitats have been evoked as an explanation for lack of genetic differences among populations of other species of butterflies (Shapiro, 1974; Brussard and Vawter, 1975).

Wilson (1965), citing Wallace (1959) and Lewontin (1961), argues that the best measure of population fitness is not the average of the relative fitness of individual genotypes, but the length of time the population persists. The application of this argument to *P. rapae* or to species with similar population structures is not straightforward. Populations in a demographic sense, as aggregations of organisms, are short-lived; however, because of extensive movements among areas of concentration and the resultant genetic uniformity, the founding and extinction of such areas within the species' range may have only minor genetic and evolutionary consequences.

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COVER ILLUSTRATION: Diagrammatic drawing of sterigma, dorsal view, of *Hipparchia fagi*, see Coutsis, page 161.

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# The Decline and Extinction of *Speyeria* Populations Resulting From Human Environmental Disturbances (Nymphalidae: Argynninae)

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**Abstract.** The fritillary butterflies of the genus *Speyeria* and their larval foodplants of the genus *Viola* (Violaceae) are among the best indicator organisms of native, undisturbed ecological communities in North America. They are also among the first organisms to be eliminated from such communities as a result of human-caused disturbances. Thus, many forms of *Speyeria* have greatly declined during the last 200 years, and several local subspecies have become extinct or are threatened with extinction. One such subspecies is *S. zerene hippolyta* (Edwards), which has recently been officially classified as a "Threatened Species" by the U.S. Department of the Interior. This paper presents a discussion of the problems of extinction in *Speyeria* butterflies throughout the United States in general, and reviews the history and problems with *S. zerene hippolyta* in particular.

This paper examines the general problem of declining *Speyeria* butterfly populations due to human environmental disturbances, and the current work to preserve the habitat of *S. zerene hippolyta* (Edwards, 1879), a butterfly officially classified as a "Threatened Species" by the U.S. Fish and Wildlife Service. For this study, samples of *Speyeria* collected in previous years were examined in the collections of the National Museum of Natural History, Virginia Polytechnic Institute and State University, the University of Nebraska, Oregon State University, and the private collections of L. Paul Grey of Lincoln, Maine, and E. J. Dornfeld of Corvallis, Oregon. In addition, field observations were conducted of *S. zerene* (Boisduval, 1852), *S. hydaspe* (Boisduval, 1869), and *S. callippe* (Boisduval, 1852) in Washington, Oregon, Idaho and California from 1960 to 1982, of *S. diana* (Cramer, 1775) in Virginia and Tennessee from 1975 to 1978, of *S. nokomis* (Edwards, 1862) in New Mexico and Arizona in 1976, and of *S. idalia* (Drury, 1773) in Illinois, Iowa and Nebraska in 1978 and 1982. During the field work, the parameters of the habitat including the floral composition and physical aspects were examined, and the probable larval foodplants were identified. The research reported in this paper of *S.*

*zerene hippolyta* was partially funded by the U.S. Forest Service in order to assist the agency in protecting and managing the remaining populations on national forest land, and is based upon the Forest Service reports by McCorkle (1980) and Hammond (1980).

## Decline and Extinction in *Speyeria* Populations

During the past 100 years, biologists and conservationists have become acutely aware of the extermination problems facing many native plants and animals in North America. Of course, the major attention has focused on the decline and extermination of large vertebrate animals such as the Passenger Pigeon, Carolina Parakeet, Whooping Crane, Ivory-billed Woodpecker, and California Condor. Such large vertebrates have declined as a result of over-collecting and the destruction of habitat and food resources. Insects are rarely affected by human over-collecting pressures due to their high reproductive capabilities, but are extremely sensitive to the destruction of their habitat and food resources (Pyle, Bentzien & Opler, 1981). The Diana Fritillary (*Speyeria diana*) of the southern Appalachians is a prime example of this. This butterfly is extremely popular with amateur butterfly collectors, but extensive collecting in parts of western Virginia for many years has not had a noticeable impact upon the populations. Instead, the drastic decline of *S. diana* during the past 200 years was largely due to the destruction of the old-growth hardwood forests in the low valleys and bottomlands for timber and agriculture (Clark & Clark, 1951). Today, the *S. diana* populations in the Appalachians appear to be quite healthy and may actually be expanding with the regrowth of the hardwood forests (Hammond observations, 1975-78).

The general American public and even many biologists with applied orientations often do not realize how extremely complex and intricate natural communities and ecosystems really are, and how extremely sensitive such systems are to human disturbances. Completely virgin, undisturbed ecological communities support a great diversity of native plants and insects. However, as human disturbance of the communities increases, the diversity of species in the communities rapidly decreases. Such activities as agriculture, extensive overgrazing by livestock, extensive forestry management for increased timber production, and suburban development are extremely destructive to natural ecological systems, and can quickly eliminate most of the native plants and insects.

The fritillary butterflies of the genus *Speyeria* and their larval foodplants, violets (*Viola*), are among the most sensitive organisms in native ecosystems, and are among the first to be exterminated as a result of widespread human disturbance. Illustrative of this is the Regal Fritillary (*S. idalia*) and its larval foodplant, the Blue Prairie Violet (*V. pedatifida* Don). These organisms are two of the most characteristic indicator species of virgin tall-grass prairie in the central United States (Hammond observations, 1978 and 1982). Like the American Bison, it is quite evident that millions of *S. idalia* must have swarmed across the vast expanses of the original tall-grass prairies in Illinois, Iowa, Missouri, Kansas, Nebraska, South Dakota and North Dakota before Europeans eliminated this native ecosystem with agriculture. Today, the violet and butterfly are mainly confined to the few small patches of virgin prairie that still survive in these prairie states, and are being preserved by state and private agencies.

*Speyeria nokomis* is a second species that has suffered serious decline in the southwestern United States due to human disturbances. The species appears to be very tightly restricted to wet, boggy meadows that have a permanent source of water throughout the summer (Hovanitz, 1970; Ferris & Fisher, 1971). Such habitats are naturally scarce in the arid Southwest, and are frequently destroyed by livestock overgrazing and water diversion. For example, meadows observed in the Sacramento Mountains of New Mexico and White Mountains of Arizona were heavily impacted by excessive livestock grazing during 1976. Likewise, the Owens Valley in Inyo County, California, has lost much of its natural water flow as a consequence of water diversion to the City of Los Angeles. Although no subspecies of *S. nokomis* appear to be in danger of extinction at the present time, the colonies are certainly far less abundant than in the past. In addition, the Mexican subspecies *S. nokomis caerulescens* (Holland, 1900) may now be extinct within the United States with the apparent loss of the Mt. Lemmon colony in Pima County, Arizona (Wielgus, 1973). There is also some concern regarding the status of *S. nokomis wenona* dos Passos & Grey 1945 of Nuevo Leon, Mexico, since this distinctive subspecies has apparently not been found in many years despite several expeditions to its habitat (McCorkle observations, 1972 and 1981).

Even very common species in widely ubiquitous habitats are heavily affected by various types of disturbance. For example, *S. hydaspe* is the primary species of *Speyeria* found in old-growth conifer forests in the Pacific Northwest. However, the timber harvest method of large clear-cuts has steadily replaced the old-growth forests with young, brushy second-growth forests during the past twenty years, steadily reducing the available habitat for *S. hydaspe* as a consequence.

Likewise, both *S. callippe harmonia* dos Passos & Grey 1945 and *S. zerene platina* (Skinner) 1897 are very common species in the sagebrush communities of the arid lowlands east of the Cascade Range. Observations made near Soda Springs and Montpelier, Idaho during 1971 and 1982 revealed a dramatic contrast between undisturbed rangelands and those heavily grazed by livestock. The ungrazed areas supported a rich diversity of herbaceous plants including the Sego Lily (*Calochortus nuttallii* T. & G.), penstemons (*Penstemon* spp.), Indian paintbrushes (*Castilleja* spp.), lupines (*Lupinus* spp.), and the Yellow Prairie Violet (*Viola nuttallii* Pursh.), together with large butterfly populations. However, the heavily grazed areas retained very few herbaceous plants or butterflies, and were mostly barren except for the remaining sagebrush.

Human disturbance has been particularly destructive to native ecological communities along the West Coast, and many forms of *Speyeria* have become extinct or are threatened with extinction in this region. A typical example is *S. adiaste atossa* (Edwards) 1890. The *atossa* populations were once widely distributed and extremely abundant in the Sierra Madre, Tejon and Tehachapi Mountains of southern California, living on open grasslands where violets such as the Pine Violet (*V. purpurea* Kell.) were abundant (Comstock, 1927). According to Emmel and Emmel (1973), the subspecies is probably completely extinct today, with the last known specimen collected in 1959. It is thought that over-grazing by livestock combined with drought so greatly reduced the larval foodplant that the butterfly could no longer survive (Orsak, 1974).

Suburban growth and development have also been extremely destructive to native violet and *Speyeria* populations, as seen in the San Francisco Bay region. At one time, three very unusual forms of *Speyeria* were endemic to this area. A very dark, melanic form of *S. coronis coronis* Behr once lived in the lowlands on the north side of San Pablo Bay in Napa and Sonoma Counties, and apparently became extinct between 1940 and 1950 (L. Paul Grey, personal communication). At about the same time, the southern pale form of *S. zerene myrtleae* dos Passos & Grey 1945 became extinct in the coastal areas of San Mateo County due to suburban development. The most widely distributed *Speyeria* around San Francisco Bay was the extremely dark, melanic *S. callippe callippe* (Boisduval) 1852, which lived on many of the higher hillsides around the bay. This species is also nearly extinct in the region today, although a few colonies still survive on San Bruno Mountain. New development projects may eliminate these colonies in the near future, resulting in the complete extinction of the once widespread *Speyeria* populations in the San Francisco area.

More widespread exterminations have taken place in the Willamette Valley of western Oregon, where the original native prairie grasslands have been almost completely destroyed due to human disturbances, including extensive agriculture, over-grazing by livestock, and the introduction of rank growing weeds and grasses that have crowded out the native plants. Many of the rarer native plants have become totally extinct in Oregon. For example, a rare yellow flowered Indian paintbrush (*Castilleja levisecta* Greenm.) is only known to survive in one large population near Tenino, Washington, but was once widely distributed from British Columbia through western Oregon (Kenton Chambers, personal communication).

A partial idea of the original flora and insect fauna of the Willamette Valley can be reconstructed through specimen records preserved in the insect and plant collections at Oregon State University. Three different species of violets were apparently widely distributed in the valley grasslands, including *V. hallii* Gray, *V. howellii* Gray and *V. nuttallii praemorsa* Dougl. Of these, *V. hallii* is apparently completely extinct in the valley and *V. howellii* is nearly extinct. *Viola nuttallii* still survives on a few of the open south-facing hills around the Willamette Valley, but the extensive populations once found on the valley floor have been completely eliminated. Two species of *Speyeria* may have utilized these grassland violets in the past. A large form of *S. callippe elaine* dos Passos & Grey 1945 apparently lived on the valley grasslands, and a few ancient specimens collected near Corvallis between 1897 and 1926 are still preserved in the O.S.U. collection today. *Speyeria zerene bremnerii* (Edwards) 1872 was largely restricted to the foothills around the Willamette Valley, and was widely distributed from the Columbia River south to Lane County near Eugene. The last known specimen of *bremnerii* was collected in 1973 near Corvallis, and this form may also be extinct in western Oregon today.

Fortunately, *S. callippe elaine, V. hallii* and *V. nuttallii praemorsa* are still very common in parts of southwestern Oregon in Jackson and Josephine Counties, while *S. zerene bremnerii* and *V. howellii* may still be fairly widespread in western Washington and on Vancouver Island. Of course, additional human developments in these regions could eventually cause the organisms to become extinct throughout their ranges, but they do not appear to be threatened with complete extinction at the present time. However, this is certainly not true of *S. zerene hippolyta* (Edwards) 1879.

## The Decline and Conservation of *S. zerene hippolyta*

The *hippolyta* subspecies of *S. zerene* is closely related to the inland valley *S. zerene bremnerii*, but it is highly specialized for living in coastal salt-spray meadows and grassy headlands at the edge of the Pacific Ocean. A few populations have also been found living on the open grasslands of high mountains located a few miles inland from the ocean. These salt-spray meadows contain many different native plants including the larval foodplant of *S. zerene hippolyta*, the Common Blue Violet (*Viola adunca* J. E. Smith). In addition to the butterfly and violet, many other native wildflowers grow in this meadow habitat. These include two species of wild orchids (*Habenaria greenei* Jeps. and *Spiranthes romanzoffiana* Cham.), wild strawberry (*Fragaria chiloensis* L.), Indian paintbrush (*Castilleja hispida* var. *litoralis* Pennell), Seaside Daisy (*Erigeron glaucus* Ker.), California Aster (*Aster chilensis* Nees), goldenrod (*Solidago* sp.), and a rare grape fern (*Botrychium multifidum* Gmel.). The most important grasses are short bunch grasses including Red Fescue (*Festuca rubra* L.), Tufted Hairgrass (*Deschampsia cespitosa* L.), and several species of bentgrass (*Agrostis* spp.). Since these grasses do not grow very tall, the other wildflowers including the violets grow easily among the grass without being shaded or crowded out.

At one time, populations of the butterfly were widely distributed in such meadows along the Oregon and Washington coasts. However, these original, native salt-spray meadows have almost completely disappeared today due to such human developments as motels and vacation homes, and due to the ecological succession and invasion of shrubs, trees and tall introduced grasses (orchard and rye grasses) into the meadows that have crowded out the native meadow plants, including the violets.

These natural grasslands are thought to have originated from burning activities by the American Indians, who apparently burned off coastal areas periodically for thousands of years to keep the coast open for their fishing and hunting activities. When European settlers arrived on the Oregon and Washington coasts, they took over the grasslands for livestock pastures, and continued such burning practices until fire prevention regulations curtailed such activities. Without fire to maintain the grasslands against brush and tree invasion, most of the coastal grasslands gradually disappeared to salal and salmonberry brushland or Sitka spruce forest. Historical photographs show that brush and forest have taken over large areas of grassland between Rock Creek and Big Creek in Lane County, Oregon, just during the last 10-20 years. Of course, the native wildflowers and butterflies disappear as the brush and trees invade and crowd out the grasslands.

Even without brush and tree invasion, the native grasslands experience a second ecological problem in the absence of fire. The dead grass leaves from previous years growth do not decay very fast in the coastal environment, and gradually accumulate to form a thick layer of thatch that smothers and crowds out the violets and other wildflowers. This is currently a very serious problem in the meadows between Rock Creek and Big Creek, and was partly responsible for the extinction of the butterfly at Ten Mile Creek a few years ago. If the grasslands were burned off every 5-10 years, this layer of dead thatch would be removed, opening up space for the violets to grow and multiply.

Today, only three large populations of typical *hippolyta* are still known to exist on the central Oregon coast, two on federal land in the Siuslaw National Forest at Rock Creek-Big Creek in Lane County and on Mt. Hebo in Tillamook County, and one on The Nature Conservancy's preserve at Cascade Head in Tillamook County. In addition, two small, weak populations were still surviving near the Camp Rilea military reservation in Clatsop County, Oregon, and on the Long Beach Peninsula near Loomis Lake in Pacific County, Washington at the end of 1982. However, the survival of both populations is currently very precarious due to the threats of ecological succession and human developments. As a result, *S. zerene hippolyta* has been officially listed as a "Threatened Species" in the U.S. Department of the Interior's Endangered Species List, effective October 15, 1980. The U.S. Fish and Wildlife Service in cooperation with the U.S.

Forest Service and The Nature Conservancy is now implementing a management recovery plan to preserve the grassland habitat of *hippolyta*, which will include fire as a management tool.

It should be noted that disjunct and slightly divergent populations of *S. zerene* possibly related to *hippolyta* are also found in high subalpine meadows of the Olympic Mountains in Washington and in coastal Del Norte County, California, north of Crescent City. For management purposes, these are not officially considered to be part of the typical *hippolyta* subspecies. They may represent ancient, relict isolates derived from *hippolyta*, or perhaps independent convergence into a *hippolyta*-like form. A distinctly different *S. zerene* race is found on the southern Oregon coast in Curry County, where it occupies typical salt-spray meadow habitats in the manner of *hippolyta*. These populations, representing an intergrade between *S. zerene behrensii* (Edwards) and *S. zerene gloriosa* Moeck, are thus located between typical *hippolyta* populations to the north in Lane County and the Del Norte County populations to the south. It is probable that these *behrensii-gloriosa* populations are a coastal intrusion from similar inland *S. zerene* populations in the Rogue River valley of Curry County. Unfortunately, the California coastal populations of *S. zerene* are facing the same threats from ecological succession and human developments as the Oregon and Washington *hippolyta* populations. These include the *hippolyta*-like populations of Del Norte County, the coastal *behrensii* populations of Humboldt and Mendocino Counties, and the *myrtleae* populations of Sonoma and Marin Counties.

*Acknowledgments.* Many people have contributed to the study of *S. zerene hippolyta* on the Oregon and Washington coasts. We are particularly indebted to Milton G. Parsons of the U. S. Forest Service for his help and encouragement with the *hippolyta* study. We would also like to thank Ernst J. Dornfeld and L. Paul Grey for their assistance and data, and John D. Lattin and Kenton L. Chambers for access to the systematic insect and plant collections at Oregon State University.

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# A New *Limenitis weidemeyerii* W. H. Edwards from Southeastern Arizona (Nymphalidae)

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**Abstract.** A new subspecies of *Limenitis weidemeyerii* is described from the Chiricahua Mountains of southern Arizona.

In their revision of *Limenitis weidemeyerii* W. H. Edwards, Perkins and Perkins (1967) noted that material from the Chiricahua Mountains in southeastern Arizona differed consistently from typical *L. w. angustifascia* (Barnes & McDunnough). Specimens collected recently by the junior author support this contention of distinctiveness; hence, the population is hereby designated:

### Limenitis weidemeyerii siennafascia, new subspecies (Fig. 1)

**Male** (based on holotype and 26 topoparatypes). The dorsal surface is essentially identical with *angustifascia*. On the ventral surface, the new subspecies differs from other *weidemeyerii* by having relatively more red-brown ("chestnut" in Smithe, 1975) overscaling, especially just proximal to the postmedian white band of the secondaries. This area is usually black with no overscaling in *angustifasia*, although some specimens show some red-brown anteriorly. There also tends to be more red-brown overscaling on the subapical area of the primaries and broader whitish overscaling bordering the submarginal red-brown spots on the secondaries of *siennafascia*, although these characters are not consistent.

**Female** (based on allotype and 7 topoparatypes). The characters which distinguish males from other *weidemeyerii* subspecies are also diagnostic for females. The red-brown overscaling of the discal area of the ventral secondaries is even more extensive and prominent.

**Size** (measurements of right primary along costal margin to farthest extent of the apex). Holotype = 34.6 mm, male topoparatypes 31.7-36.4 mm, x all males = 33.8 mm (N = 24). Allotype = 37.9 mm, female topoparatypes = 37.6-40.1 mm, x all females = 38.3 mm (N = 7). The new subspecies averages smaller than *angustifascia* (male = 36.4 mm, female = 42.9 mm, from Perkins and Perkins, 1967).

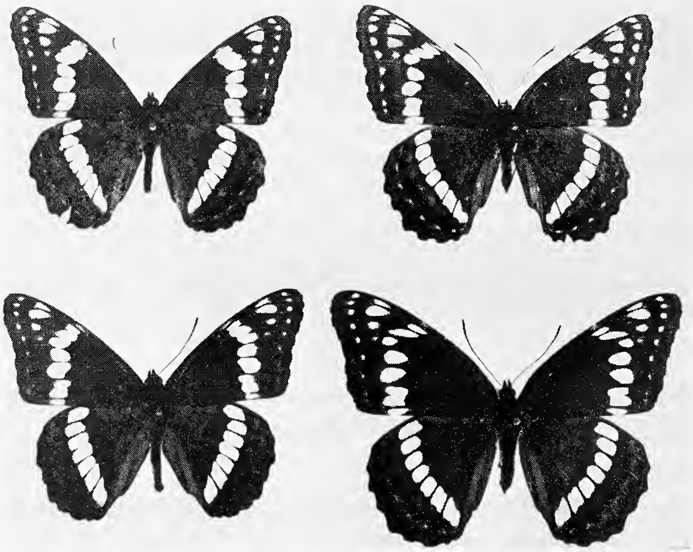

Fig. 1a. *Limenitis weidemeyerii* subspecies, dorsal surface. Left top: male *siennafascia*—holotype, bottom: male *angustifascia*—AZ: Coconino Co.; Oak Creek Canyon, ca. 6000′, 12 June 1979. Right top: female *siennafascia*—allotype, bottom: female *angustifascia*—AZ: Apache Co.; White Mts., Ditch Camp, 5 July 1980.

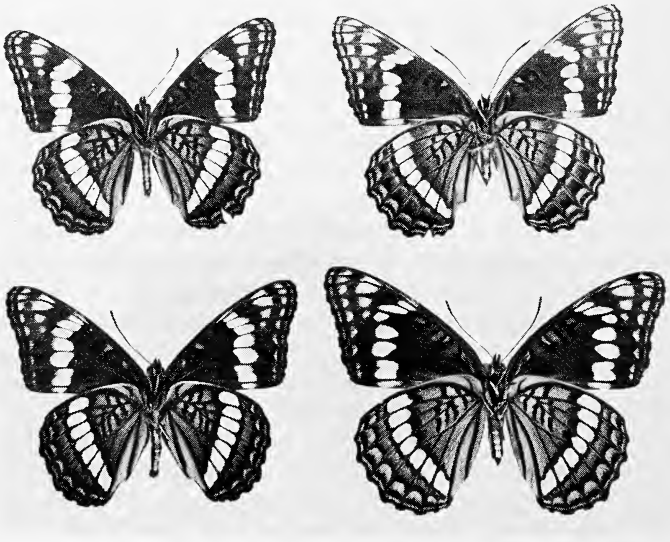

Fig. 1b. *Limenitis weidemeyerii* subspecies, ventral surface. Same specimens as Fig. 1a.

**Types.**[1] Holotype: S(outh)E(ast) A(ri)z(ona), Cochise Co(unty), Chiricahua M(oun)t(ain)s, n(ear) Barfoot P(a)rk, 8400′, June 14, 1981, leg. D. Mullins. Allotype: same data as holotype except July 13, 1980. Topoparatypes: 5♂♂ 1♀ with same data as holotype; 8♂♂ 6♀♀ with same data as allotype; 13♂♂ same data as holotype, except June 26, 1982.

**Type Locality**. ARIZONA: Cochise County; Chiricahua Mountains, near Barfoot Park, 8400′ (T17 S, R30E, S33). The north-facing slopes at this elevation are a Spruce-Fir association in which there are patches of Quaking Aspen (*Populus tremuloides*). The latter serves as the foodplant (*fide* K. Roever).

**Deposition of type material**. The holotype and allotype will be deposited in the type collection at the Allyn Museum of Entomology, Sarasota, Florida. Two ♂ and one ♀ topoparatypes are in the senior author's private collection. A pair each of topoparatypes will be deposited in the following museums: American Museum of Natural History, New York; Los Angeles County Museum; Smithsonian Institution, Washington, D. C.; and Instituto de Biologia, Mexico, D.F. The remaining topoparatypes are retained in the junior author's private collection.

**Other specimens examined** (All ARIZONA: Cochise Co.; Chiricahua Mountains). E. side Chiricahua Mts., Price Canyon, 15 July 1968, 2♂♂, 26 July 1975, 1♂, leg. ?; on road near Barfoot Park, 5 July 1981, 1♂ 1♀, 26 June 1982, 6♂♂, leg. M. Smith; Barfoot Park, 8000′, 19 June 1960, 2♂♂, 1 July 1961, 3♂♂, 12 July 1970, 3♂♂ 2♀♀, 3 July 1976, 3♂♂, leg. K. Roever; Barfoot Park, 3 July 1976, 1♂, leg. J. Werner; Pinery Canyon, 6950′, 3 July 1976, 1♂, leg. J. & S. Werner. Perkins and Perkins (1967) mention a number of additional localities from the Chiricahua Mountains. The new subspecies should be searched for in adjacent western New Mexico and northern Mexico.

**Etymology**. The name *siennafascia* describes the distinctive red-brown overscaling of the ventral surface and is in keeping with names proposed for other *weidemeyerii* phenotypes (e.g., ab. "sinefascia" Edwards, *angustifascia* and *latifascia* Perkins and Perkins).

## Discussion

*Limenitis weidemeyerii siennafascia* is at once distinguished from all other *weidemeyerii* taxa by its relatively extensive red-brown overscaling on the ventral surface, especially on the secondaries of the female. Because of this, *siennafascia* shows no sharp demarcation in ventral pattern, whereas this surface in *angustifascia* is crisp and clear. Much of the overscaling seems to be rather quickly lost in flown individuals. The new subspecies tends to have more individuals with orange spotting on the dorsal secondaries (38% of the sample vs. 18% in *angustifascia*, Perkins

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[1] Data as on specimen labels, parenthetical data clarify label data.

and Perkins, 1967) and white in the cell of the dorsal primaries (57% vs. 33%). The presently known range of *siennafascia* in the Chiricahua Mountains is separated from other *weidemeyerii* populations by some 130 km to the northeast (Pinos Altos Mts., Grant Co., New Mexico) and by over 160 km to the north (Blue Range, Greenlee Co., Arizona).

*Acknowledgments.* We thank Kilian Roever for information on the foodplant. Kilian Roever, Mike Smith and the Southwestern Research Station made their collections available for examination, for which we are grateful.

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# Semispecies Relationships between *Heliconius erato cyrbia* Godt. and *H. himera* Hew. in Southwestern Ecuador

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**Abstract.** A suture zone between *H. erato cyrbia* and *H. himera* has been found in southwestern Ecuador. Presumably $F_1$ and at least $F_2$ hybrids have been captured, but their frequency is much lower than expected in the case of random mating and most individuals of the two parental taxa show no sign of hybridization. It is concluded that they behave as semispecies. The evolutionary significance of these observations is discussed.

## Introduction

Very widespread in the neotropical region, *Heliconius* butterflies are the best studied in this area. Amongst them, the two muellerian mimics *H. erato* (L.) and *H. melpomene* (L.) have given rise to many detailed studies, both in the field of genetics (Turner and Crane, 1962; Sheppard, 1963; Emsley, 1964; Turner, 1972) and that of evolutionary systematics (Emsley, 1965; Brown, Sheppard & Turner, 1974; Brown, 1979).

The taxonomical situation of *H. erato* is especially complex in Ecuador, where the species is represented by ssp. *lativitta* Btlr. in the Northern part of the Amazonian lowlands and ssp. *etylus* Salv. in the southern part of the same region. The two taxa are very much alike. On the contrary, in the upper part of the Pastaza valley, ssp. *notabilis* Salv. and God. flies and looks extremely different. However, *lativitta* and *notabilis* interbreed freely in the transition region, giving rise to all possible intermediate and recombined phenotypes (Descimon & Mast de Maeght, 1971). On the Pacific slopes, the species is represented by ssp. *cyrbia* Godt., which is strikingly distinct from the Amazonian subspecies. The continuity of the specific complex was demonstrated by Emsley (1964, 1965), both through laboratory crosses and biogeographical studies.

The taxonomic status of *H. himera* Hew. is less well understood. This taxon is endemic to southern Ecuador and adjacent Peru, associated with dry forest and semi-arid conditions. When we wrote our article about the *Heliconius* of Ecuador in 1971, we quoted that species from Rio Engano, a small stream running down from the Cerro de Abitagua, near Puyo. Actually, we were misled by a synonym: there is another rio of this name in southern Ecuador—in Spanish, Engano means "error"!. Thus, the quotation of *H. himera* from the Pastaza region is a mistake and all the considerations developed in our paper are irrelevant. In fact, fifteen days after it was published, we became aware of the real ecology of the butterfly, which we observed in great numbers in the region of Jaen, Amazonas, northern Peru, together with many of the characteristic endemics of the "Maranon dispersion center" (Mueller, 1973), such as *Battus streckerianus* Honr., *Diaethria ceryx* Hew. and many more. Even though Brown (1979) cited some localities where either *cyrbia* or *etylus* are reported together with *himera*, no data were provided about the form of the contact. Thus, the taxonomic structure of the *erato* complex is uncertain in southern Ecuador; Lamas (1976), quoting unpublished data of Brown, Benson, Gilbert and Lamas, as well as Brown (1979), consider *erato* and *himera* as conspecific, but without presenting facts. Moreover, it was not specifically stated whether the oriental or the occidental populations of *erato* are considered.

The southern region of Ecuador is unique in all the Andes in that the Cordillera is sufficiently low to allow faunal exchanges. it was this phenomenon that we intended to study in our 1971 travel in northern Peru. Actually, we were bitterly disappointed, because faunal exchanges between the lowland moist forest regions of both sides are hindered by the presence of an extensive semi-arid zone, the above mentioned "Maranon center", which acts as an efficient barrier.

The dry forest faunas fly on both sides of the watershed and penetrate (at least partially) the basin of the Rio Catamayo and that of the Rio Tumbes. In the upper part of the latter (Rio Puyango), a very clearcut contact between an extensive area of dry forest and a tongue of moist premontane forest was observed in January 1975 by H. Descimon. This zone is cut by the road Loja-Catamayo-Portovelo *ca* 8 km above the small village of Guayquichuma, at an elevation of 1200-1400 m. The zone is also clearly detectable on the very good ecological map of the Atlas del Ecuador (1982). In that locality, a single *Heliconius* was seen, flying at the bottom of an inaccessible glen, which looked like a *cyrbia* x *himera* hybrid. In spite of some efforts, it could not be secured, and no other individual be found in the neighbourhood.

In July 1982, the authors, together with F. Lafite and H. D.'s family, undertook a journey to southern Ecuador, one of the main objectives of which was to clear up the *himera-cyrbia* problem. The Rio Puyango locality had not changed; two small valleys separated by *ca.* 2 km were explored and were actually the only two accessible biotopes with some remnants of

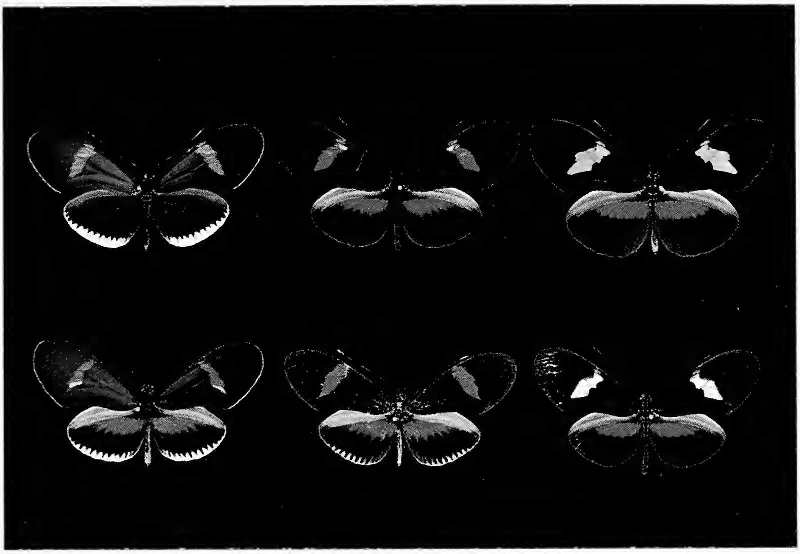

Fig. 1. *Heliconius* from southwestern Ecuador
**1.** *H. erato cyrbia*, male. Guayquichuma, Dept. el Oro, 200782. **2.** *H.* "lafitei" (*himera* x *cyrbia*), same locality, 190782 (No. 1). **3.** *H. himera*, same locality, 200782. **4.** *H.* "clarae" (probably "lafitei" x *cyrbia*), same locality, 200782 (No. 4). **5.** *H.* "clarae", same locality, 210782 (No. 5). **6.** *H.* "petri" (probably "lafitei" x *himera*), same locality, 190782 (No. 6).

forest. Both upwards and downwards along the road, all slopes become dryer and degraded, and the moist forest disappears.

All over western Ecuador, *H. erato cyrbia* was on the wing, while *H. melpomene* was very scarce—a fact in contradiction with our previous assumptions (Descimon & Mast de Maeght, 1971) and the widespread opinion that *H. melpomene* is commoner than *H. erato*. An explanation would be that *H. erato* flies more during the dry season and *H. melpomene* more during the rainy season, in western Ecuador at least—a possibility that should be checked by more numerous observations.

The first Heliconians to be seen in the Guaquichuma glen were typical *cyrbia*, but a *himera* was readily observed in the same place. Then, three hybrids were caught successively by F. Lafite. A total of 31 pure *cyrbia*, 11 *himera* and 6 hybrids were caught by the six collectors and in three days of serious efforts. All hybrids were males.

## Description

The hybrids fall into three clearcut categories. Their main characteristics, compared with those of the parent butterflies are given in Table 1 and illustrated in Figure 1. Since giving Linnean names to hybrids is not allowed by the International Code of Zoological Nomenclature, we will

Table 1. Comparative features of *Heliconius erato cyrbia, H. himera* and of their hybrids from Southwestern Ecuador.

| | Upperside background | FW upperside transverse band | HW upperside "dennis" bar | HW upperside white margin | HW underside bar |
|---|---|---|---|---|---|
| *H erato cyrbia* | vivid blue iridescence | red, distal, narrow | absent | white with black veins | yellow |
| *H. himera* | black | greenish yellow, wide | red, large, almost straight distad | absent | absent, some dull red scales |
| hybrid "lafitei" | raven blue-black iridescence | red with few anterior white scales, intermediate shape | red, large, somewhat serrate distad | absent | absent, dull red scales |
| hybrid "clarae" | vivid blue iridescence | as in *cyrbia*, with a few posterior white scales | red, large, serrate distad | white, with prominent veins | very large, red basad white distad |
| hybrid "petri" | black | white slightly tinged yellow, anterior red scales | red, large, a little serrate | absent | absent, dull red scales |

designate them by mere "nicknames", which will honor our young and enthusiastic companions Frederic Lafite, Pierre Descimon and Claire Descimon.

a. *H. erato cyrbia* x *himera* "lafitei"
Deep blue background, forewings upperside with a transverse band, red with a few anterior white scales, a red band on the upperside of hindwings, which have no white margin. No. 1, 8 km above Guayquichuma, dept el Oro, Ecuador, 1200 m, 190782, F. Lafite leg.; No. 2, same date; No. 3, 10 km above Guayquichuma, 1250 m, 200782, J. Mast de Maeght leg.

b. *H. erato cyrbia* x *himera* "clarae"
Mostly alike *H. erato cyrbia*, but with a large red transverse ("dennis") band on the hindwing upperside; this band is more serrate distally than in *H. himera*. On the underside, the hindwing transverse bar is large, red basally and white distally, a feature that is not observed in any other form. No. 4, 10 km above Guayquichuma, 1250 m, 200782, H. Descimon leg. No. 5, same locality, 210782, same collector. This individual has a white marginal band darkened by black scales.

c. *H. erato cyrbia* x *himera* "petri"
Mostly like *himera*, but the forewing transverse band white with only a very faint yellow tinge and a border of red scales, mostly distal. 8 km above Guayquichuma, 190782, No. 6, F. Lafite leg.

Except for individual No. 3, all insects are in H. Descimon's coll. and will be given to the Museum National d'Histoire Naturelle in Paris. No. 3 (coll. J. Mast de Maeght) will be given to the British Museum.

## Discussion

When two parapatric taxa show a contact zone, it is generally possible to determine whether they are mere subspecies of a single species, or belong to two distinct specific units.

In the first case, a "hybrid zone" (Short, 1969) is observed, with a complete blending of the genetic pools. Such a case is indeed observed in the populations of *H. erato notabilis* and *H. erato lativitta* of the lower Pastaza region. In the second case, no actual genetic exchange takes place and the two populations remain completely distinct, even if $F_1$ hybrids casually occur with a noticeable frequency.

However, less clearcut situations are often noticed ("suture zones" of Remington, 1968), where a limited gene exchange is observed: both taxa remain distinct, with a restricted amount of intermediates, which are not limited to $F_1$ hybrids. Such taxa, neither species nor subspecies, are usually designed by the term "semispecies"—though Bernardi (1980) has clearly demonstrated that the correct name applying to these relations is "quasispecies"—it must be added that this taxon is considered by

Bernardi as *intra*specific.

In the present case, it is possible to assume, with a reasonable certainty, that the three butterflies designed under the nickname "lafitei" are $F_1$ hybrids. They are indeed approximately intermediate between *H. erato cyrbia* and *H. himera*, and especially so by phenetic characters such as the background color and the shape and position of the forewing transverse band. The other characters fit also well with what is known about their inheritance, thanks to the work of Emsley (1964) on the crossing of *H. erato cyrbia* and *H. erato adanus*. On the contrary, it is hard to assign also "clarae" and "petri" to $F_1$ hybrids. The former would better correspond to a backcross "lafitei" x *erato cyrbia* and "petri" to a backcross "lafitei" x *himera* or even to an almost typical *H. himera* with a few *erato cyrbia* genes.

In the absence of laboratory crosses, these assignments remain of course tentative, but we believe that they are far the most likely. They would suggest that the $F_1$ hybrids are not sterile and thus that there is not a complete barrier of genetic incompatibility between *H. erato cyrbia* and *H. himera*.

It is clear that, in the restricted area where we have met them together, both taxa do not behave as mere subspecies. Would they have done so, a thorough gene exchange would have produced many more intermediates than observed. For instance, in the conditions of a stationary equilibrium and assuming constant the proportions of the parents in the previous generation, a neutral homogamy situation would have produced 25 *erato cyrbia*, 3 *himera* and 17 "lafitei" (if these are assumed to be $F_1$ hybrids), instead of 31, 11 and 3, respectively observed ($X^2 = 33$, $P < 0.01$). Thus, already at the level of $F_1$ hybrid production, at least some of these prerequisites are not present. One may add that the number of "clarae" and "petri" is also inferior to that expected for backcrosses assuming the frequency of *erato cyrbia, himera* and "lafitei" to be constant (5 and 2 instead of 2 and 1 observed).

It is also difficult to assume *H. erato cyrbia* and *H. himera* to be fully distinct species. In this case, indeed, hybrids would have been at least rarer and limited to $F_1$—hybridization not implying gene exchange (Bigelow, 1965). So, no matter the mechanisms leading to this situation, both taxa should be considered as "semispecies" (*sensu* Lorkovic, 1955, and not *sensu* Mayr, 1940).

Such situations are always distressing both to systematicians and to geneticists. It is hard to conceive why hybridization, even limited, does not lead to a complete blending of the gene pools. In the present state of affairs and in practically all the known "semispecies" cases, the answers remain speculative. Moreover, laboratory results may by no means always be transposed to natural situations.

A first class of explanation commonly put forward is ecogeographical: the two taxa "brush each other" in much too restricted an area to produce an equilibrium; their phenology and habitat choice do not allow the cohabitation to be more than episodical; the meeting of the populations is too recent to have produced either a fusion of the gene pools or a selective elimination of the illegitimate mating tendencies. "Semispecies" would thus be often man-made artefacts, resulting from the destruction of natural barriers (Woodruff, 1973). Such arguments appear somewhat relevant in the present case; one may only object that hybridization occurred already 7 years ago and during the opposite half of the year. In the cohabitation zone, the extent of which is possibly much larger than was actually explored, the two taxa were intimately mixed.

A second type of explanation involves some kind of impairment of the selective value of the hybrid phenotypes. Concerning "muellerian protection", which might be lowered in hybrids, it must be noted that this factor does not hinder an active gene exchange in other "hybrid belts", such as that of the Pastaza, for instance. Altered physiological viability of hybrids between a taxon mainly adapted to wet forest and another one adapted to semi-arid forest, "hybrid breakdown" (Oliver, 1979), lower efficiency in mating and sexual attraction, partial sterility are among the most obvious factors which are usually quoted.

As Bernardi (1980) stressed, the study of "semispecies" (quasi and vicespecies, according to the terms he and ourselves consider correct) is of strategic importance to clear up the mechanisms of speciation. However, in the present case, and though *Heliconius* are becoming the best genetically known butterflies, one may cast doubts about the observational and experimental facilities offered by populations flying in remote parts of southern Ecuador, while it is already difficult to reach conclusive evidences in more accessible countries.

The only somewhat feasible and significant approach to the problem may be provided by electrophoretic analysis, which would afford much more refined data about the actual gene flow between both populations and their degree of divergence.

Otherwise, it would of course be very interesting to carry out comparative studies upon a possible (and probable) contact between *H. himera* and *H. erato etylus* in the eastern region.

*Acknowledgments.* We are most indebted to Nadia Venedictoff who welcomed and helped us during our travels. Frederic Lafite assisted us in collecting with a high efficiency and Arlette, Pierre and Claire Descimon endured the conditions of our journey with patience and courage and participated also in the collecting with willingness. Thanks to Francois Michel for his advice and the revision of the manuscript and to Keith S. Brown for his very useful criticisms. This paper is integrated within the activity of the R.C.P. N° 317 "Polymorphisme, speciation, mimetisme" of the C.N.R.S., France.

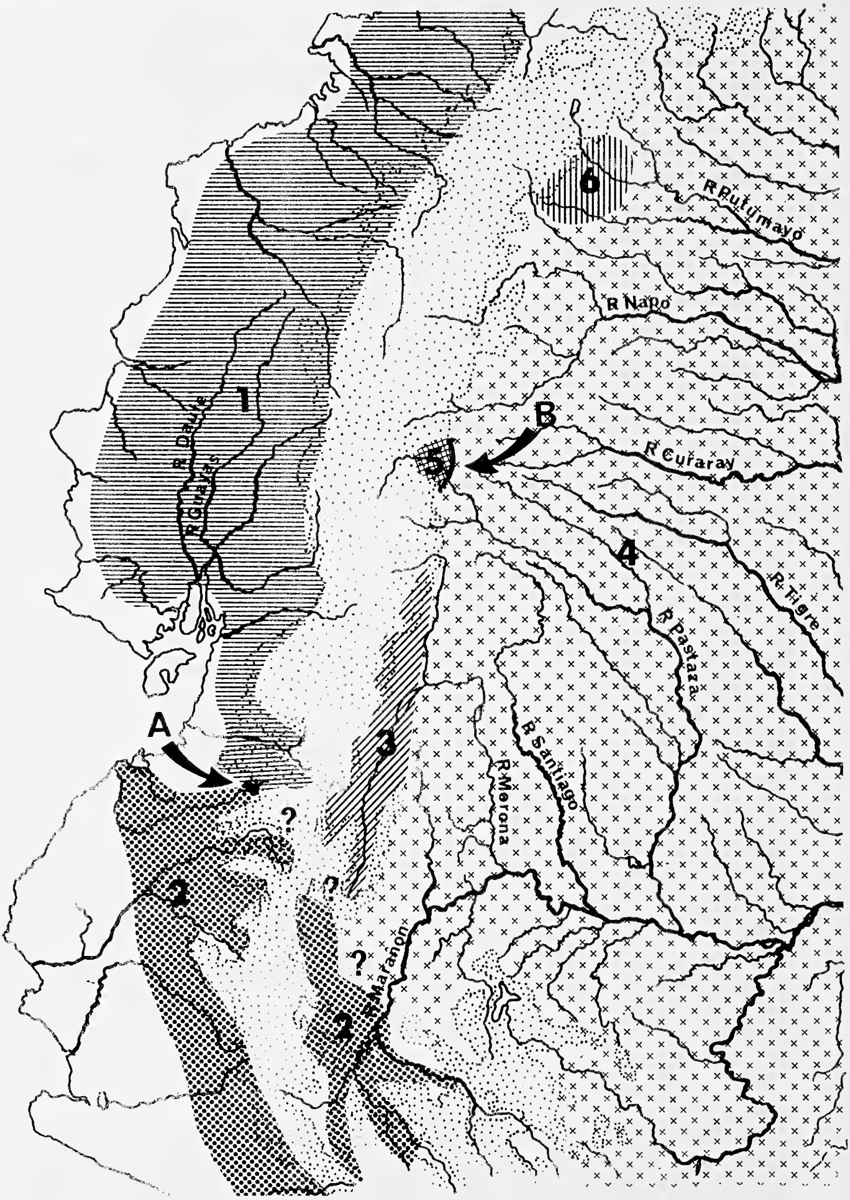

Fig. 2. Distribution of the subspecies and semispecies of *Heliconius erato* in Ecuador and the adjacent regions of Peru and Colombia.
**1.** *H. erato cyrbia* **2.** *H. himera* **3.** *H. erato etylus* **4.** *H. erato lativitta* **5.** *H. erato notabilis* **6.** *H. erato dignus* **A.** Suture zone of Guayquichuma **B.** Hybrid belt of the Pastaza region.

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# Karyotypes of some Indian Noctuid Moths (Lepidoptera)

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**Abstract.** Chromosome study during meiosis in eleven species of Indian noctuid moths (*Achaea janata, Acontia intersepta, Anomis sabulifera, Cosmophila erosa, Earias fabia, Heliothis armigera, Hyblaea puera, Plusia orichalcea, Plusia signata, Sesamia inferens, Tarache tropica*) established the haploid number as 31 in all the species. The structure and behaviour of the chromosomes during the meiotic cycle and the possible chromosome evolution in this family have been examined.

## Introduction

The latest review on Lepidopteran chromosomes (c.f. Robinson, 1971) includes spcies belonging to family Noctuidae. Karyotypes of additional species have been determined in recent years including some Indian species (Rishi, 1973, 1975; Nayak, 1975). The present paper incorporates additional information on the cytologenetics of eleven species of Indian Noctuid moths.

## Material & Methods

All the materials were collected in close vicinity of Bhubaneswar and were identified by Z. S. I. staff of Calcutta. For ease of reference, the species along with their host plants, have been listed in Table 1. The males were found to be most active meiotically in the 3rd to 5th instars. The larval testes were dissected out in hypotonic solution (0.45% sodium citrate solution) and fixed overnight in 1:3 acetic alcohol. Permanent squash and smear preparations of the material were made and the slides were stained in Heidenhains' iron-alum haematoxylin. Slides were examined under a Meopta Binocular Research Microscope and good metaphase stages were scored using 100X oil immersion objective and 15X ocular with the help of camera lucida. Some of the stages were photomicrographed.

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## Table 1

| Sl. Number | Family (Noctuidae) & Species | Foodplant |
|---|---|---|
| 1 | *Achaea janata* Linn. | *Ricinus communis* |
| 2 | *Acontia intersepta* Guen. | *Hibiscus esculentus* |
| 3 | *Anomis sabulifera* Guen. (Jute looper) | *Choreorus* sp. |
| 4 | *Cosmophila erosa* Hubn. (Green semi-looping larva) | *Hibiscus esculentus* |
| 5 | *Earias fabia* Stoll. | *Hibiscus esculentus* |
| 6 | *Heliothis armigera* Hubn. | *Cicer arietinum* |
| 7 | *Hyblaea puera* Cram. | *Tecona grandis* |
| 8 | *Plusia orichalcea* Fabr. | *Brassica oleracea* |
| 9 | *Plusia signata* Fabr. | *Nicotiana* sp. |
| 10 | *Sesamia inferens* Walk. (Pink borer) | *Eleusine coracana* |
| 11 | *Tarache tropica* Guen. | Unidentified |

## Observations

### *Achaea janata*

2n = 62. Early meiotic prophase chromosomes, especially the diplotene and diakinetic bivalents were of particular morphological interest showing a fuzzy contour, similar to Lamp-brush chromosomes. However, at late diakinesis and metaphase stages, these fringes disappeared. Metaphase I cells usually showed 31 bivalents, but very often contained several univalents. This situation even occurred in many diakinetic cells in which some of the separated elements showed chromatinic interconnection between pairs and they did not resolve completely. This further shows that the unpaired chromosomes had undergone normal segregation and were the homologues of bivalents which formed no chiasma or weak chiasma. Metaphase II showed 31 univalents (Figs. 1-3).

### *Acontia intersepta*

2n = 62. Metaphase I cells showed 31 bivalents. In some of these cells, precocious resolution of a bivalent into univalents was marked. At anaphase I, which is very short-lived, separation of homologues was synchronous, although in a good number of plates partners of a bivalent still lagged behind on the equator when all others had almost reached the poles. This may be presumed as the XX-sex chromosome pair, making inferences drawn from other sources. Metaphase II showed 31 univalents indicating the regular segragation of unpaired elements of metaphase I (Figs. 4-6).

*Anomis sabulifera*

2n = 62. Metaphase I cells showed 31 bivalents. Precocious separation of a bivalent into two univalents was noticed in a number of pro-metaphase and metaphase I cells. Both in early and mid-anaphase I, two separating elements of one bivalent, presumed as the sex-bivalent, still remained on the equatorial plate when all other bivalents had their homologues moving towards the poles. Even in some late anaphase and early telophase stages the two separated elements were seen to be present on the bridge of the spindle fibres joining two daughter nuclei under formation. If this pair is the same that as with lagging anaphasic movement, then it could be equally argued to represent the products of 'elimination chromatin' to be ultimately lost. Metaphase II showed 31 univalents confirming the haploid number as n = 31 (Figs. 7-9).

*Cosmophila erosa*

2n = 62. Metaphase I cells showed 31 bivalents but cells with 30 bivalents were also observed. In some cells, one bivalent had been resolved into two univalents (indicated by their small size) resulting in 32 elements. In two late anaphase I cells, separating elements of a bivalent exhibited the characteristic lagging behaviour. Metaphase II plates showed 31 univalents (Figs. 10-12).

*Earias fabia*

2n = 62. In some of the spermatogonial cells, two of the chromosomes (sex-chromosomes?) were more deeply stained. Metaphase I cells showed 31 bivalents, one of which was more deeply stained than the rest. In some of the cells, in equatorial view, 32 elements were observed where one of the bivalents had undergone early resolution into small-sized homologues. Intermediate forms were also noticed where components of this bivalent did not part but remained connected to one other at one point. In the ensuing anaphase, separation of the sister chromosomes were quite synchronous in every bivalent. Metaphase II plates showed 31 small univalents (Figs. 13-15).

*Heliothis armigera*

2n = 62. Metaphase I cells showed 31 bivalents. One of the bivalents had undergone early resolution and such resolution was also noticed even in some pre-metaphase plates. Anaphase I was normal but certain dividing cells exhibited two late separating elements (may be the homologues of a bivalent) on the equatorial region. Metaphase II showed 31 univalents (Figs. 16-18).

*Hyblaea puera*

2n = 62. Two of the elements, probably sex-chromosomes, were differentiated either by heteropycnotic behaviour or by their association with each other by chromatinic interconnection. Metaphase I cells showed 31 bivalents, out of which one bivalent (presumed to be the sex-bivalent) was quite often more deeply stained. In one early metaphase I cell, one bivalent was ring-like due to delayed condensation. In several metaphase I cells, early resolution of a bivalent into its homologues was noticed. Metaphase II cells showed 31 univalents (Figs. 19-21).

*Plusia orichalcea*

2n = 62. The number of metaphase I bivalents was 31. One of the bivalents (sex-bivalent?) appeared to be more intensely stained. In some cells an early separation of a bivalent into homologues was encountered. In anaphase I all the bivalents separated synchronously, although occasionally, two separating elements of a bivalent, probably the sex-bivalent, still remained together on the equatorial plate while the remainder moved towards the poles. In many late anaphase-I cells an irregular and clumped chromatinic mass was found in between the separating chromosomes. This clumped mass might be the 'elimination chromatin' although its occurrence has been reported early in the females. Metaphase II cells showed 31 univalents (Figs. 22-24).

*Plusia signata*

2n = 62. Metaphase I cells showed 31 bivalents, out of which early separation of a single bivalent was seen in many cells while resolution of a number of bivalents into univalents was marked in others. Occasionally, in addition to bivalents and univalents a number of "ringforms", perhaps due to chromatinic interconnections between the ends of separating homologues of bivalents, were observed. Again, rarely, almost all bivalents were found to have resolved into their homologues before onset of anaphase. In anaphase I, separation of homologues was more or less synchronous although, in a number of anaphase cells, one bivalent or the resolved elements of it, showed lagging movement and remained in between the separating groups of chromosomes. Metaphase II cells showed 31 univalents (Figs. 25-27).

*Sesamia inferens*

2n = 62. Metaphase I cells showed 31 bivalents. Certain cells, however, contained more than 31 chromosomes, possibly due to early resolution of some of the bivalents. A number of tetraploid cells with double the number of bivalents of normal spermatocytes were also recorded. In almost all the anaphase I cells, the bivalents separated into two equal halves simultaneously, although in certain cells one bivalent (or two separating elements probably homologues of the sex-bivalent) still lingered on the equatorial region when the remaining separated chromosomes nearly reached their respective poles. Late anaphase I chromosomes resolved into their chromatids as they reached the poles. Metaphase II cells showed

31 univalents (Figs. 28-30).

*Tarache tropica*

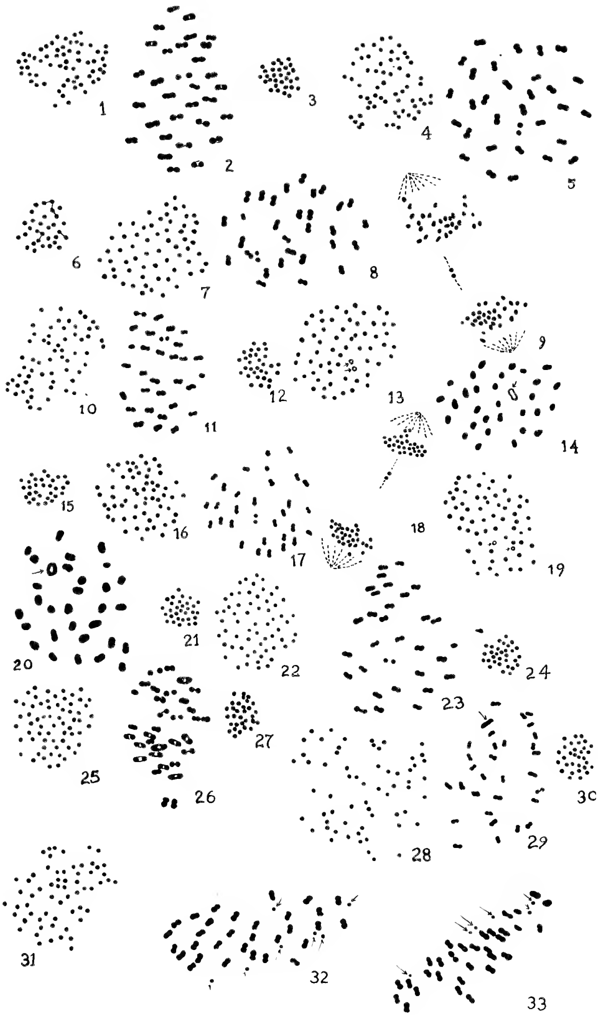
2n = 62. In addition to 31 bivalents, one pre-metaphase cell contained 3 minute dot-like chromosomes which were very likely of supernumeraries. Besides the normal 31 bivalents, metaphase I cells showed a variable number (3 to 7) of minute chromosomal elements. These minute elements, could be either true supernumerary chromosomes or the non-homologous unpaired chromosomes of interspecific hybrids, the latter not uncommon in nature. Distinct metaphase II cells were rare (Figs. 31-33).

## Discussion

White (1973) emphasized the need for studying the chromosomes of insects since cytogenetics has contributed to insect systematics in several ways as species which are not always morphologically differentiated can be ascertained as distinct species when difference is noted in their karyotype. Very little attention has been paid to the study of the cytology of Lepidoptera, although much work in this group has been carried out on ecology and control of pests. To be specific, information on the chromosome numbers of Lepidoptera is available for about only one percent of the total number of species of this order. In India, studies on this aspect are negligible. The reason the study of Lepidoptera chromosomes is neglected include:

1. The chromosomes are extremely small, oval, dot-like or almost spherical, or isodiametric and compact bodies yielding no information regarding the position of the centromere and other morphological details.
2. Chromosomes show a marked tendency of clumping together.
3. Ill-defined meiotic stages.
4. Anomalous nature of centromere and sex-chromosomes.

That the Lepidopteran chromosomes, except for minor differences in size, present remarkable uniformity in morphology and behaviour during the meiotic cycle have been well documented (Seiler, 1914; Beliajeff, 1930; Federly, 1938; Lorkovic, 1941; Gupta, 1964; Suomalainen, 1969; Rishi, 1973, 1975; Nayak, 1975; Ennis, 1976). The present investigations confirm earlier findings in that the chromosomes are homomorphic, minute-sized elements presenting a circular disposition both in mitotic and meiotic metaphase stages. A high chromosome number (2n = 62) found in the species investigated is not uncommon for the haploid chromosome number in Lepidoptera extends between 7 in *Erebia aethiopellus* (de Lesse, 1959b) to n = 223 in *Lysandra atlantica* (de Lesse, 1970). In majority species of the group the haploid number falls between 29 to 31. Beliajeff (1930) considers 30 as the ancestral number both for Lepidoptera and Trichoptera which have many features in common including a diffuse centromeric activity, female heterogamety, lack of visible chismata



Figs.1-3. Chromosomes of *Achaea janata.*
Figs. 4-6. Chromosomes of *Acontia intersepta.*
Figs. 7-9. Chromosomes of *Anomis sabulifera,*
Figs. 10-12. Chromosomes of *Cosmophila erosa.*
Figs. 13-15. Chromosomes of *Earias fabia.*
Figs. 16-18. Chromosomes of *Heliothis armigera.*
Figs. 19-21. Chromosomes of *Hyblaea puera.*
Figs. 22-24. Chromosomes of *Plusia orichalcea.*
Figs. 25-27. Chromosomes of *Plusia signata.*
Figs. 28-30. Chromosomes of *Sesamia inferens.*
Figs. 31-33. Chromosomes of *Tarache tropica.*

in the female, occurrence of elimination chromatin in the first meiotic division of the egg, the formation of apyrene sperms and the occurrence of close modal haploid number. Virkki (1963) considers 60 to be modal diploid number. On the other hand White (1954, p. 176) considered 31 as the most frequent haploid number in the members of the group studied to that date with 29, 30 and 31 so nearly equally frequent that he did not feel any of these numbers to be considered as the type number in preference to the others. In the present investigations, chromosome numbers of all the eleven species of the noctuids have a haploid chromosome number n = 31 which agrees with the modal haploid chromosome number (n = 31) established for this family and for Lepidoptera in general (Saitoh, 1959; Bigger, 1960, 1961; Gupta, 1964; Robinson, 1971; Saitoh *et. al.*, 1971; Nayak, 1975).

Very few species of Lepidoptera have been reported so far to have chromosomes as supernumerary elements in their karyotype (Maeki & Makino, 1953; de Lesse, 1960, 1967; Maeki & Ae, 1966; de Lesse & Brown, 1971; Bigger, 1976; Rao & Murty, 1976; Nayak, 1978; Padhi & Nayak, 1981(82)). It is, of course, difficult to distinguish genuine supernumerary chromosomes in the Lepidoptern karyotype which might include a large number of highly contracted chromosomes or even early resolved minute univalents. In the present report, *Tarache tropica* shows numerical variation of 3 to 7 supernumeraries in its karyotype. The number varies from cell to cell and from follicle to follicle. Robinson (1971) considers supernumerary elements as small segments of normal chromosomes produced by accidental breakage. In Lepidoptera, since fragmentation is a common aspect of chromosome evolution, the origin of supernumeraries, as held by him, no doubt, is a special case since the produce of such accidental breakage is likely to behave as a normal chromosome of the regular karyotype in the absence of any localised centromere. Bigger (1976) reported the presence of ß-chromosomes in British material of both *Pieris rapae* and *Pieris napi* and is of the opinion that the supernumeraries are true additional chromosomes and not small fragments of the normal karyotype. Although the exact mode of supernumerary origin is debatable we are of the same opinion as that of White (1973) who considers them to have arisen through fragmentation of heterochromatic blocks of normal chromosomes and to have no evolutionary role in the increase of chromosome number.

Information on the sex-chromosomes of Lepidoptera is meagre since in most species they are not distinguishable from the autosomes. However, there is a female heterogamety with XO or XY females and XX males. Seiler (1958) reports both XO and XY females in *Solenobia triquetrella*. A heteropycnotic pair of chromosome associated with the nucleolus during the spermatogenesis in *Philosamia cynthia* was considered as the sex-chromosome pair by Kawaguchi (1937). Kurihara (1929) had a similar opinion in *Bombyx mori*. Others considered the deeply stained feulgen positive body sometimes associated with the nucleolus during the indescrete diplotene, as well as the autosomal elements clumped together due to non-specific stickiness, as the sex-chromosome pair (Federley, 1913; Seiler, 1914; Kernewitz, 1915; Gupta, 1964). A pair of chromosomes larger than others frequently occurring in species with high chromosome numbers have been considered as the sex-chromosomes by many workers (Bauer, 1943; White, 1954, 1973; Suomalainen, 1969, 1971). Ennis (1976), investigating chromosome numbers of Canadian Lepidoptera, observed the frequent occurrence of a similar larger pair in a number of lower chromosome numbered taxa, suggesting that in many species the larger pair merely represent an autosomal fusion product. Bigger (1975) found in his observations in *Polyommatus icarus* and *Pieris brassicae* that the largest chromosome is only marginally larger than the other large chromosomes compared with those of other butterflies. Thus size alone cannot be the parameter to distinguish the sex-bivalent. Traut and Mosbacher (1968) distinguished sex-chromatin as a distinctly heteropycnotic body in the somatic interphase nuclei in the females of 70 out of 83 species examined and took it as the Y-chromosome, since the presence of such body was not observed in the corresponding males. Traut and Rathjens (1973) used the fluorescent Feulgen technique to demonstrate the W (= Y) chromosome in the early oocyte and nurse cells. Suomalainen (1969) demonstrated the occurrence of distinct sex-chromatin bodies in somatic tissues of females of *Witlesia crataegella, Scoparia ambigualis* and *Bactra robustana* and suggested this to be the heteropycnotic Y-chromosome. Bigger (1975), by employing G-banding technique, furnished strong evidence in support of the sex-chromatin body as the X-chromosome in *Pieris brassicae* and *Polyommatus icarus* where in a small proportion of interphases he clearly observed a heteropycnotic body which corresponded very closely to the structure of G-banded X-chromosomes. In the present work, confined to male germinal cells, with their XX-sex chromosomes it is difficult to distinguish the equal sized XX-sex chromosome pair in most cases. However, in few cases a relatively larger bivalent, as discussed above, has been observed in *Earias fabia* and *Sesamia inferens*. If the opinions of Bauer (1943), Suomalainen (1969), White (1973) and Ennis (1976) are to be taken as correct, we may consider the larger bivalent in such species as the XX-sex chromosome pair. Further in some of the species, with all small chromosomes of equal size, a peculiar type of lagging behaviour at anaphase-I has been shown by one chromosome pair as in *Acontia intersepta, Anomis sabulifera, Cosmophila erosa, Heliothis armigera, Plusia signata* and *Sesamia inferens*. This pair may be suspected as the XX-sex chromosome pair, but the point requires further investigation.

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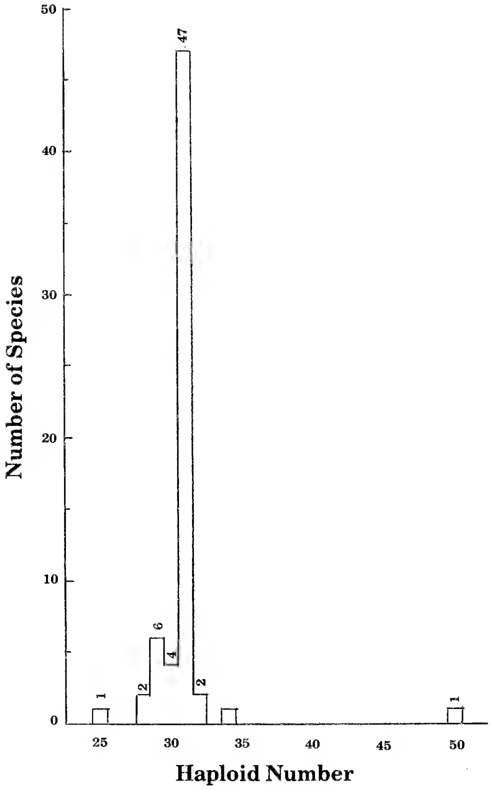

Fig. 34. Histogram showing haploid chromosome number in Family Noctuidae.

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# Courtship Leading to Copulation in the Cloudless Sulphur, *Phoebis sennae* (Pieridae)

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**Abstract.** The components and temporal structure of courtship leading to copulation are described for the cloudless sulphur, *Phoebis sennae* Linnaeus. Hand-reared virgin females were tethered and placed near a nectar source to elicit male interest and courtship behavior. The courtship is like that described for several other pierids in that the male buffets the female with his wings for a few seconds before alighting and attempting copulation. Females either remain motionless or may perform a brief rejection behavior before becoming motionless and accepting the male.

## Introduction

During copulation, a male butterfly passes accessory gland secretions into the female's reproductive tract and these secretions are used by the female for her own nutritional purposes (Boggs, 1981; Boggs and Gilbert, 1979; Boggs and Watt, 1981). Rutowski *et al.* (1983) described the interspecific variation in the size of this nutrient investment made by males for ten species of butterflies. It was argued in that paper that the males of these ten species do not vary substantially in the size of the investment and that this is correlated with a lack of variation in their courtship behavior. In particular the investment does not appear to vary between species in a way that reflects differences in the intensity of mate choice from species to species. This paper is one in a series describing the previously unknown courtships of species whose nutrient investments were discussed. In particular this paper describes the courtship behavior leading to copulation for the cloudless sulphur, *Phoebis sennae* Linnaeus.

## Methods

The cloudless sulfur was studied from July to November of 1981 at the Archbold Biological Station 13 km south of Lake Placid, Florida. Virgin females were reared from larvae collected in the field from the coffee sennae, *Cassia occidentalis* Linnaeus. Rearing techniques and conditions were like those described for *Eurema lisa* Boisduval and LeConte in Rutowski (1977). Within 2 days after eclosion females were tethered and placed on an exposed perch in or near a large planting of pagoda flower (*Clerodendrum paniculatum* Linnaeus) that was regularly visited by males and females of *P. sennae.* A tether constituted a 1 m long piece of cotton thread, one end tied around the base of the female's abdomen and the other end to a nearby plant. Interactions leading to copulation between these virgins and males were filmed using a Beaulieu 4008 ZM 2 super-8 movie camera at the 24 (most interactions) and 70 (a few interactions) frame per sec settings. All summary statistics are given as mean ± standard deviation.

## Results

Twenty-one courtships leading to copulation were filmed using 5 virgin females. As many as 6 copulations with a single female were obtained by separating the pair as soon as possible after coupling and then returning the female to the perch and permitting her to mate again. Of the 21 film records three involved courtships with more than one male and so were disregarded in these analyses. Another was also disregarded because the female changed perch during the courtship and although she was followed with the camera it was not possible from the film to see the necessary details.

Courtship began when the male approached the female and made contact with her wings with either his wings or legs, or when the female responded to the male approach by opening her wings either briefly in a wing flick or for some time in a mate refusal posture (Obara, 1964). In only three courtships did the female not open her wings at some time during the interaction. If the female assumed a mate refusal posture it was not uncommon for the male to land on the female's wings. After this or before the male alit the female closed her wings and the male moved into position along side the female with his head pointing in the same direction as the female's. The male then curled his abdomen out from between his wings which were flapping throughout this time and began attempting to insert his abdomen up between the female's hindwings. Coupling could not be directly observed but its occurrence was assumed to be accompanied by a cessation of wing flapping by the male. However, within a second or two after the male closed his wings he began strong wing beats and initiated a post-nuptial flight in which he attempted to carry the female to another perch. In all cases, however, the tether obviously prevented the male from carrying out his intentions.

In 5 courtships the male's first attempt to couple was unsuccessful as indicated by the fact that he stopped probing at the female's hindwings with his abdomen and shifted to the other side of the female before probing again. In four of these instances the second coupling attempt was successful while in one the male was not successful until his third attempt.

For purposes of temporal summary the beginning of courtship was taken as when the female opened her wings in response to the male's approach or when the male first made contact with the female, which ever came first. The end of courtship was taken as when the male closed his wings and became still or, if he did not do that when he began the strong wing beats that marked the beginning of the post-nuptial flight. The mean duration of all filmed courtships then was 6.87 ± 4.65 sec (n = 17; range = 2.96 - 22.3). The large standard deviation reflects the pooling of courtships that varied in structure. For example, for courtships in which the male successfully coupled in his first attempt and in which the female did not perform a mate refusal posture the duration was 4.83 ± 1.26 sec (n = 8; range = 3.5 - 6.58 sec). Also, courtships in which the male performed more than one copulation attempt but in which the female did not have her wings open for more than 2 sec total during the courtship were of significantly greater duration (7.43 ± 1.28 sec (n = 4); t 3.71, 12 df, p <0.002) by 2 to 3 sec than courtships in which the male attempted copulation only once.

The responses of females to males varied from remaining still with the wings closed to strong and prolonged mate refusal postures. In one courtship the female performed a mate refusal posture for more than 7 sec during the courtship. However, in most (65%) the female performed a flutter response or mate refusal posture that lasted less than 2 seconds. Obviously the duration of courtship is to some extent affected by the amount of time the female has the wings open during the courtship but it was not statistically demonstrable with this data set. However, the two longest courtships were also those in which females performed lengthy mate refusal postures but also those in which the male attempted copulation 2 or 3 times.

Contact by the male or wing opening by the female were convenient and clear markers of the beginning of courtship but in a variety of cases the male hovered for a second or so over the female before he touched her or the female responded. This hovering appeared similar to what the male does when courting flying females before they alight.

Unsuccessful courtships took one of two forms with perched females. In the first, the male departs although the female has assumed an apparently receptive posture with the wings closed. In the second the male is prevented from attaining copulation by the female who persistently performs a mate refusal posture and he finally departs. This was observed a number of times even with the hand-reared virgin females. The male's response to this posture was usually to land on the dorsal wing surfaces and move around in an attempt to attain the position required to couple.

## Discussion

The courtship of *Phoebis sennae* is strikingly similar in form and temporal structure to that described for several other pierids including *Eurema lisa* (Rutowski, 1978), *Colias eurytheme* Boisduval, *C. philodice* Godart (Silberglied and Taylor, 1978), *Pieris protodice* Linnaeus (Rutowski, 1979), and several members of the genus *Pieris* that occur in Japan (Suzuki *et al.*, 1977). In all these species, the typical pattern is that the male approaches a perched female and buffets her with his wings briefly before alighting and attempting to couple with her. If the female is flying and receptive when the male approaches she alights quickly and courtship proceeds as described. In some pierids the male performs a special display before attempting to couple with the female (*Eurema daira* Latreille: wing waving display (Rutowski, in press); *Nathalis iole* Boisduval: wing spread display (Rutowski, 1981(83)). Although displays of this sort were not observed in successful courtship in *P. sennae* the overall courtship durations were not substantially different from those observed in species with these displays. Hence, as suggested in Rutowski *et al.* (1983) the courtship of this species does not depart in overall structure and complexity from that observed in most species of butterflies (see Silberglied, 1977; Scott, 1973).

Among the species of *Phoebis* that are sympatric in the neotropics there are striking differences in the structure of the supposed scent-producing structures (Klots, 1951, pers. obs.) and in the patterns of ultraviolet reflectance found on the male's dorsal wing surface (Allyn and Downey, 1977; Silberglied, 1979). *Phoebis sennae* males have no ultraviolet reflectance and a very indistinct sex brand. It would be of interest to determine if the variation in ultraviolet reflectance patterns and scent-producing structures found in these sulphurs are correlated in any way with variation in courtship behavior.

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# Biosystematics of the *Euphydryas* of the Central Great Basin with the Description of a New Subspecies

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**Abstract.** The taxonomic status of Great Basin *Euphydryas* is discussed. Widespread *E. anicia wheeleri* oviposits on *Castilleja chromosa* in pinyon-juniper habitats. *E. editha lehmani* also oviposits on *C. chromosa* and co-occurs with *wheeleri* in a more restricted distribution. Additional populations of *E. editha* occur in alpine habitats in the Toiyabe, Schell Creek, and Snake Ranges of Nevada. These butterflies oviposit on *Castilleja lapidicola* and are described here as a new subspecies, *Euphydryas editha koreti.*

## Introduction

In many otherwise well-curated collections of butterflies in major institutions in North America there exists considerable confusion surrounding the taxonomic status of Great Basin *Euphydryas*. Specimens of two species, *Euphydryas anicia* (= *chalcedona*, Scott, (1978) and *E. editha*, are commonly misidentified as one another. There are several reasons for this mix-up including 1)the subspecific names themselves, which refer to both people and places, 2)confusion over the type localities and the geographic distribution of subspecific taxa involved, 3)the great phenetic similarity of the two species where they are sympatric, and 4) the broad sympatry and synchrony of both species, coupled with the ecological and genetic differentiation of one species *E. editha* into two distinct ecotypes.

The purpose of this paper is to unravel some of this taxonomic confusion, first, by identifying the taxa involved, their distributions and what is known of their host plant associations, and, second, by naming a new subspecies of *Euphydryas editha* which is ecologically, genetically and phenetically distinct. A large part of the overall confusion stems from the previously unnamed status of this ecotype.

## Distributions

Two ruddy, moderate-sized checkerspot butterfly species are found in the widespread pinyon-juniper-sage scrub of the central Great Basin at elevations between 1600 m and 2500 m. Both species are univoltine, passing winter in diapause as fourth instar larvae, and flying between mid-

May and late June. The two butterflies have distinct but broadly overlapping distributions. *Euphydryas anicia wheeleri* ranges from central Utah (including the Deep Creek and Stansbury Ranges and the western Wasatch Plateau) west to western Nevada (the Stillwater Range, White Mountains, and the Sweetwater Range) where it blends morphologically with what is known as *E. chalcedona macglashanii*, and south from northern Nevada's Pequop Mountains to the Wilson Creek Range, also in Nevada. The distribution of *Euphydryas editha lehmani* is considerably more restricted (Fig. 1). It co-occurs with *E. anicia* in the Toiyabe, Monitor, Toquima, White Pine, Egan, Schell Creek and Snake Ranges of Nevada (the county records of these butterflies are listed by Harjes, 1980). *E. editha gunnisonensis* occurs east of the Wasatch Plateau of Utah and is virtually identical to *lehmani* in all characteristics.

On the high alpine slopes of Wheeler Peak in the Snake Range a small "*nubigena*-like" *Euphydryas editha* ecotype is found at elevations nearly 1500 m above the pinyon-juniper belt. Populations of this butterfly are known only from alpine areas of the Snake Range (Wheeler Peak, Bald Mountain, and the Moriah Table), Schell Creek Range (North and South Schell Peaks) and Toiyabe Range (Bunker Hill). It may also occur in the as yet uncollected alpine of the Deep Creek Range in Utah.

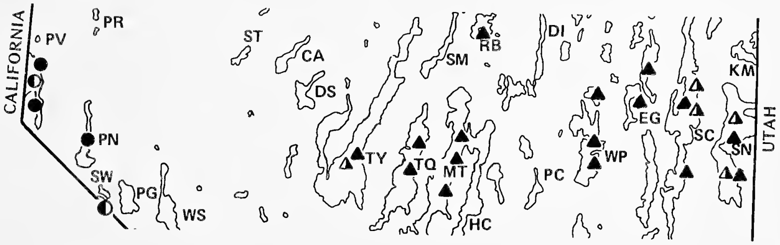

Fig. 1. Distribution of Central Nevada *Euphydryas editha* subspecies: filled circles - *E. editha monoensis*, half-filled circles - *nubigena*, filled triangles - *lehmani* and half-filled triangles - *koreti*. Initials provide identification of ranges for use with conventional map (i.e. EG = Egan Range, PN = Pine Nut Mountains, etc.).

## Nomenclature

Most of the confusion arises from numerous samples collected in the Wheeler Peak area of the Snake Range. Here *Euphydryas anicia wheeleri* is common near Lehman Caves, at about 2200 m, while the most frequently collected *E. editha* in the area is taken high, at above 3700 m, on Wheeler Peak. This high elevation insect is not *lehmani*, though the name has been often applied to it.

Like the mountain itself, the naming of *Euphydryas anicia wheeleri* was a memorial to George M. Wheeler, the leader of a series of U.S. Geographic surveys of this area in the late nineteenth century. The butterfly was named in 1881 by Henry Edwards from specimens taken by members of the expedition. The type locality of *E. anicia wheeleri* iss "Southern Nevada" and was inferred by Bauer (1975) to be from somewhere west of Belmont, Nye County, Nevada, at least a couple of hundred miles from Mt. Wheeler.

Jean Gunder (1929) described *Euphydryas editha lehmani* from specimens provided by Frank Morand also from the immediate vicinity of Lehman Caves, Nevada. The types, in the American Museum of Natural History, are labeled Mt. Wheeler, White Pine County, Nevada. However, the phenotype and capture date, VI-4-29, clearly imply a location low on the mountain. The latinized suffix indicates that this *E. editha* subspecies also was named for the person, Absolom Lehman, an early local resident, rather than the place.

## Biology

Through much of their ranges *Euphydryas anicia wheeleri* and *E. editha lehmani* oviposit nearly exclusively on *Castilleja chromosa*, a widespread paintbrush, which is apparently hemiparasitic on the ubiquitous sagebrush, *Artemisia tridentata*. In addition, *Euphydryas anicia* frequently oviposits on *Pedicularis centranthera* in the Lehman Caves area and infrequently on *Penstemon speciosus* in the White Mountains. *Euphydryas editha lehmani* commonly oviposits on *Castilleja linariifolia* in the Pequop Mountains, and infrequently on *P. centranthera* in several ranges. Both butterflies have been recorded nectaring most often on *Senecio multilobatus* and less often on *Erigeron argenteus* and *E. blommeri*.

The male genitalia can be used to separate the two species. In *Euphydryas editha* the valvae have two obvious arms separated by an angle of greater than 90°. The upper arm is much shorter than the lower. In *E. anicia* this angle is considerable less than 90° and the upper arm nearly approaches the lower in length (see Ehrlich and Ehrlich, 1961 and Dornfeld, 1980). Other more superficial characters (listed in order of value) can be used with some confidence to differentiate *E. anicia* and *E. editha* in the Great Basin:

1. A row of white spots on segments 2-7 are found in the dorsal part of the plural region of the abdomen of most *E. anicia*. These may be limited to fewer segments or, rarely, may be totally obscured. *E. editha* never have these spots.

2. *E. anicia* are significantly larger than *E. editha*. Mean forewing length of 20 male *E. anicia* from the Monitor Range is 20.5 mm (s.d.=1.0); Toquima Range, 19.8 mm (s.d.=0.6); Roberts Mountains, 21.8 mm (s.d.=1.0) and Quinn Canyon Range, 20.5 mm (s.d.=0.9). Forewing length of 20 male *E. editha* from the Monitor Range is 17.3 mm (s.D.=1.1); Egan

Range, 17.6 mm (s.d.=0.9); Spruce Mountain, 17.7 mm (s.d.=0.7) and White Pine Range, 16.8 mm (s.d.=0.9). From the Monitor Range, *anicia* are larger than *editha*, $p<<0.0001$. Pooling the 80 individuals of each species from 4 different ranges, *anicia* are also larger than *editha*, $p<0.0001$.

3. Cell CU2 of the forewing is largely solid red on the ventral surface of *E. anicia*. Markings are normally completely lacking in the extra-mesial and mesial bands and first and second over-innermarginal spots (see Burdick, 1958). Only the marginal section of this cell usually is marked with cream or yellow. In contrast the CU2 cell of *E. editha* is well marked with black, red and yellow or cream spotting.

4. The male forewing is distinctly more acute at the apex in *E. anicia* than *E. editha*. The specimen of *E. anicia wheeleri* illustrated in Howe (1975) is not typical in this regard (nor in ground color, the specimen being extremely dark); the forewing shapes of the illustrated males of *E. chalcedona corralensis* and *E. anicia morandi* in the same volume are closer to typical *wheeleri*.

5. Where sympatric, *E. anicia* normally fly slightly earlier than *E. editha* resulting in a condition on the average more worn in the former species. The overlap of flight in both time and space, includes nearly complete synchrony and sympatry during extended flight periods at White Sage Canyon in the Monitor Range. In contrast, Snake Range *Euphydryas anicia* fly on dry slopes and ridges and appear up to several weeks earlier than *E. editha*. While *E. editha* adults are isolated in meadows along Baker Creek, both species are found at meadow margins.

## **Euphydryas editha koreti** Murphy and Ehrlich **new subspecies**
## **Koret's Checkerspot**

Diagnosis. The key characteristic separating this subspecies from others in the Great Basin is size. Twenty males from the Snake Range have a mean forewing length of 14.4 mm (s.d.=1.2) and from the Schell Creek Range 15.4 mm (s.d.=0.9), significantly smaller than other Great Basin *Euphydryas*.

As in all individuals of this species, the dorsal and ventral surfaces of the wings are marked with transverse rows of red, yellow and black spots (Fig. 2). The best character for discriminating this new subspecies from other alpine *E. editha* is on the dorsal hindwing. The outer row of spots (the marginal band) is red as in all *Euphydryas*. This row is bordered basad by a narrow black band, then by a band of yellow spots or chevrons (the submarginal band) in most individuals. (This submarginal band is normally red in Sierra Nevada *E. editha nubigena*.) The next band inside (extramesial band) is red, the next (mesial band) is yellow but may be suffused with red though not to the extent or in as many individuals as *nubigena*. In most *nubigena* all three outer bands of the hindwing are red.

Forewing markings are less consistent but show a similar trend toward increased yellow spotting. Again the outer marginal band is red. The next inner band is yellow, sometimes suffused with red. (In nearly all *nubigena* this second band is red.) A

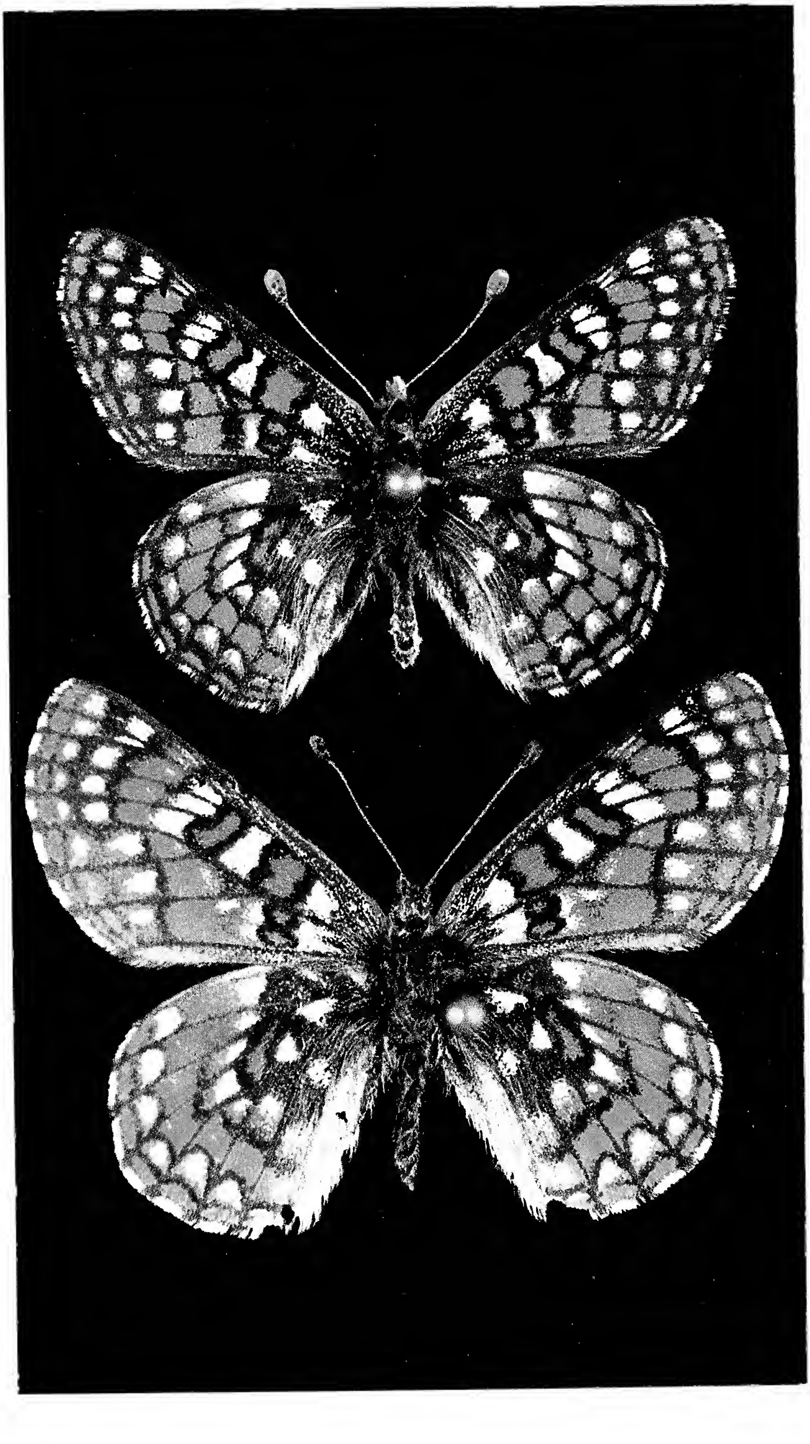

Fig. 2. *Euphydryas editha koreti*, Murphy and Ehrlich, male above, female below.

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broad dark band separates this from a third, wider band of yellow spots. (These spots though yellow are comparatively reduced in *nubigena*.)

Hindwing interspot bands are usually complete, relatively thick and very dark brown to black. Both dorsal and ventral wing markings of *koreti* are as a result more clear, well separated and well defined than those of any other alpine *Euphydryas* including *E. anicia eurytion, E. editha nubigena, remingtoni, lawrencei* or *beani*.

TYPES: **Holotype male:** Nevada, White Pine County, Ridge south of Bald Mtn., 16 July 1980 (G.T. Austin).

**Allotype female:** Same data. Types: Deposited in the American Museum of Natural History (AMNH).

**Paratypes:** 70 ♂♂ and 16♀♀. Nevada: *White Pine Co.*, 5♂♂, Ridge above Stella Lake, 11,000′, 30 July 1979, G.T. Austin; 32♂♂, 9♀♀, Ridge south of Bald Mtn., 16 July 1980, G.T. Austin; 6♂♂, 2♀♀, Bald Mtn., Snake Range, 24 July 1969, P. Herlan; 21♂♂, 4♀♀, summit North Schell Pk., Schell Creek Range, 17 July 1980, D.D. Murphy; *Lander Co.*, 4♂♂, Mahogany Canyon, [Toiyabe Range], 2 August 1971, P. Herlan; 6♂♂, 1♀, Bunker Hill, Toiyabe Range, 22 July 1982, B.A. Wilcox.

Pairs of paratypes deposited at the AMNH, California Academy of Sciences, Los Angeles County Museum, and the United States National Museum. The remainder of the type series is in the private collection of George T. Austin, in the collection of the junior author at Stanford University, and in the Nevada State Museum, Carson City, Nevada.

This subspecies is named in honor of the late Joseph Koret, in deep appreciation of his support, through the Koret Foundation, of our research.

## Discussion

This new subspecies is an ecological analogue of *Euphydryas editha nubigena* from the central Sierra Nevada, occurring abundantly on alpine and subalpine mountaintops and ridges. Females of *E. e. koreti* exclusively oviposit on *Castilleja lapidicola*, a dwarf paintbrush resembling the larval host of more northern *nubigena* populations, *Castilleja nana*. Both subspecies, by virtue of habitat, fly late into the summer. *E. editha koreti* rarely appear before July even in extremely dry years, and often fly well into August in wet years. Adult males may hilltop well above and away from oviposition sites on ridge saddles and summits. Both sexes may be found nectaring as low as the upper margins of the pinyon-juniper forest. Nonetheless, the more than a month difference in peak flight times, larval host choice differences, and up to one mile vertical separation of habitat centers presumably are effective in keeping *E. editha koreti* and *E. editha lehmani* from exchanging genes.

Some preliminary genetic information is available on *Euphydryas editha koreti* (Wilcox, Ehrlich and Murphy in prep.). *Koreti* populations exhibit the highest fraction of monomorphic loci among some 60 populations of the species sampled across more than a dozen named subspecies. This condition, which has been viewed as indicative of a high degree of isolation, fits our understanding of the geographic distribution of *koreti*. Populations of this subspecies are few in number and extremely isolated in Great Basin Ranges. And, the likelihood of genetic exchange between populations or of natural colonizations of now uninhabited alpine areas, given this present distribution, is vanishingly small.

The genetic distance, as determined by Rogers' index (1972), among alpine Great Basin and Sierra Nevada *Euphydryas editha* populations for 20 structural gene loci shows generally more similarity among the Basin and Sierran groups of populations than between them. However, whether *Euphydryas editha koreti* has a polyphyletic origin is not clear. A scenario where lower elevation populations of *E. editha lehmani* gave rise to extremely convergent high elevation forms independently in each range seems unlikely but not impossible. However, that analysis awaits completion of locus by locus comparisons of high and low elevation populations which are in progress.

The survival of this new subspecies probably has benefitted from the relative inaccessability of its habitat which is distant from urban areas and is topographically extreme. It thus has low potential for agriculture, grazing or most development. But threats to the critical habitat of *E. editha koreti* do exist. The ranges of this region are thought to have substantial mineral potential. For this reason the Schell Creek Range was denied wilderness designation and the Snake Range slated for "further planning" despite the overwhelming biological and scenic value of the regions (USDA, 1979). Clearly, the present atmosphere in the U.S. Department of Interior makes the possibility of creating a Great Basin National Park, as was once proposed for the Snake Range, effectively zero. The combined effects of the extremely narrow range limits of this newly described subspecies and a potential mineral rights free-for-all in its habitat poses a very real threat to Koret's Checkerspot.

*Acknowledgments:* We thank George T. Austin of the Nevada Museum, Las Vegas, for providing much of the museum material for this study; his generosity and intimate knowledge of Nevada butterflies has been of immeasurable value in our ongoing studies of Great Basin butterflies. Bruce A. Wilcox and Oakley Shields provided some of the specimens for electrophoresis. Pam Higby provided expert isozyme analysis at Langmuir Labs at Cornell University. Karin Mahr kindly aided in preparation of this manuscript. Support for this study came from NSF grants DAR 80-22413 and DEB 78-22413.

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UNITED STATES DEPARTMENT OF AGRICULTURE, 1979. Rare II. Roadless area review and evaluation.

## Notes

### A Recessive Lethal "Wingless" Mutation in *Tatochila* (Pieridae)

Bowden (1963, Entomologist 96:52) reported the occurrence of an apparently recessive lethal mutation in *Pieris napi* L., producing wingless and legless pupae. A somewhat similar but doubtfully homologous mutation affecting the pupal wings has occurred twice in the laboratory culture of the Andean-Patagonian *Tatochila sterodice* Stgr. species-group, maintained at Davis for four years. It was first noted in a line of pure Chilean *T. mercedis* Esch. derived from pooled ova of several females from **Vicuña,** Coquimbo in 1979. This stock was overall rather unhealthy, and the "wingless" pupae which appeared in several families of the second generation were attributed to pathology and discarded (although no similar pupae had been seen in previous Pierid cultures). The unhealthy subcultures were terminated, and no further "wingless" pupae were seen until 1983 In November 1982, a new line of pure *mercedis* was established, from pooled ova of several females collected in metropolitan Santiago. By this time no Chilean *mercedis* genes were in the culture, but *mercedis* from the Province of Neuquén, Argentina, had been incorporated in several hybrid subcultures with no "wingless" pupae having appeared. The first lab generation of Santiago *mercedis* was completely healthy, but a very few "wingless" pupae were noted in the second, derived from the pooled progeny of three sib matings. In the third, 6/33 pupae reared under continuous light and continuous high temperature (24L, 27°C) were "wingless," but this was again a pooled lot from two sib matings. Further breeding was confined to families which had shown no "wingless" pupae.

A first-generation male *mercedis* of the new Santiago line was mated to a female of complex hybrid ancestry involving Argentine *mercedis, sterodice, vanvolxemii* Capr., and Ecuadorian *arctodice* Stgr. The resulting brood was vigorous and contained no "wingless" pupae. Seven sib matings were obtained within this brood. In the first, Sib A, "wingless" pupae occurred under both rearing regimes used (24L, 27°C: 15/48; 10L14D, 23.9°/12.8°C: 6/42) (total 21/90). No other "wingless" pupae were observed in the other sib matings, including the very large (over 250) Sib C, except one in the small Sib F (which could conceivably represent an accidental egg- or larval transfer from Sib A). All the sib broods were reared side-by-side under the same conditions in the same growth chambers on food from a common source, and were handled only by the author using standardized, uniform procedures. Only a few subcultures from this overall brood of over 1000 animals were made, and families containing "wingless" pupae were again not bred.

Larvae which give rise to "winglesss" pupae are apparently normal. Unlike Bowden's trait, the legs are not directly affected, nor are the wings truly missing. Instead, the wing-*cases* are wholly missing, so the wing sacs are everted and convoluted. The lack of the wing-cases apparently causes more or less deformity of the proboscis- and leg-cases for purely mechanical reasons. Typical examples are shown in Fig. 1. None of the ventral thoracic structures is fully or properly hardened, but the head and thoracic dorsum are normal or nearly so. Most of the "wingless" pupae die within 4 days, but a few have progressed to the pharate adult but failed to emerge. In these pigment was not laid down in the wings but was normal elsewhere.

Fig. 1. Three "wingless" pupae from brood Sib A showing variable degree of deformity on the ventral surface. Note partially everted wing sacs. Two of these pupae reached pharate adult status before dying. (Photograph by S. W. Woo.)

No attempt was made to do the formal genetics of this trait. However, the above data are all consistent with the interpretation of "wingless" as a Mendelian recessive lethal. The source of the second allele in the sibs derived from the complex hybrids mated to pure *mercedis* is uncertain, but it is suggestive that the trait has only appeared in crosses deriving from *mercedis* and has never been seen, for example, in pure *vanvolxemii* although over 1,000 have been reared. Although nutritional problems can cause somewhat similar deformities in Pierids reared on artificial diets, the uniform food sources and rearing conditions argue against such causation in our pupae. Wing deformity is a common and non-specific indicator of infection by bacteria or viruses. Again, the rearing conditions argue against infection, but the possibility—especially of latent or transovarial infection—cannot be excluded. An anonymous reviewer of this paper reports (*in litt.*) the occurrence of a similar condition in a mass culture of *Pieris brassicae* L.: "The wing cases were totally absent and the leg- and antenna-cases strongly reduced." The condition, whose causation was apparently not demonstrated, was confined to two subcultures and was eliminated when they were terminated in the third generation.

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## A Revised, Annotated Checklist of World Libytheidae

### Family Libytheidae Duponchel 1844 (= Libythaeidae Lucas 1899)

A. Genus *Libythea* Fabricius 1807 (type = *L. celtis* Fuessly 1782, designated by Latreille 1810). Synonyms are *Hecaerge* Ochsenheimer 1816, *Chilea* Billberg 1820, *Hypatus* Huebner 1822, and *Dichora* Scudder 1889 (type = *L. labdaca* Westwood 1851). Misspellings include *Lybithea* Rafinesque 1815, *Libythaeus* Boitard 1828, *Lybathea* Edwards 1874, and *Libethea* Wolcott 1936.

1a. *L. geoffroy alompra* Moore 1901 (= *hauxwelli* Moore 1901)—Burma, Tenasserim, Laos, Thailand.
b. *L. geoffroy antipoda* Boisduval 1859 (= *quadrinotata* Butler 1877)—New Caledonia, Lifu (Loyalty Islands).
c. *L. geoffroy bardas* Fruhstorfer 1914—Luzon, Mindoro, Cebu, Mindanao, Negros.
d. *L. geoffroy batchiana* Wallace 1869 (= *batjana* Fruhstorfer 1909/10)—Obi, Buru, Batjan, Halmahera, Morty, Sula Magoli.
e. *L. geoffroy celebensis* Staudinger-Boisduval 1859—Celebes, Macassar, Sula.
f. *L. geoffroy ceramensis* Wallace 1869 (= *seramensis* Fruhstorfer 1909/10)—Ceram, Amboina, Java.
g. *L. geoffroy deminuta* Fruhstorfer 1909/10—Babar, Damar, Wetar.
h. *L. geoffroy eugenia* Fruhstorfer 1909/10—New Guinea, Biak, Borneo, Fergusson, Kai, the Key Islands.
i. *L. geoffroy genia* Waterhouse 1938—NW coast of Australia (Darwin to Condillac and Cassini Islands).
j. *L. geoffroy geoffroy* Godart 1820 (= *geoffroyi* Wallace 1869)—Thailand, Java, Portugese Timor, Timor, Sula, Kepulauan Kangean.
k. *L. geoffroy howarthi* Petersen 1968—Rennell (Solomons).
l. *L. geoffroy maenia* Fruhstorfer 1909/10—Waigeu, Biak, Key Tual, Mysol, New Guinea.
m. *L. geoffroy nicevillei* Olliff 1891 (= *myrrha* Macleay 1866)—NE coast of Australia (Banks Island to Magnetic Island), Lord Howe Island.
n. *L. geoffroy orientalis* Godman & Salvin 1888—Guadalcanal, Bougainville, Choiseul, Kulambangra, Manam, Nissan, Rendova, Ysabel (Solomons).
o. *L. geoffroy philippina* Staudinger 1889 (= *philippensis* Fruhstorfer 1909/10)—Palawan, Mindanao, Camguin de Mindanao, Panaon, Bohol, Ticao (Philippines).
p. *L. geoffroy pulchra* Butler 1882 (= *neopommerana* Pagenstecher 1896)—New Britain, New Ireland.
q. *L. geoffroy sumbensis* Pagenstecher 1896—Sumba, Sumbawa.
2. *L. collenettei* Poulton & Riley 1928—Nuka Hiva (Marquesas Islands).
3a. *L. narina canuleia* Fruhstorfer 1909/10—North Celebes.
b. *L. narina luzonica* Semper 1889—Luzon, Mindanao, Palawan.
c. *L. narina nahathaka* Fruhstorfer 1914—Ceram, Amboina, Buru.
d. *L. narina narina* Godart 1819 (= *hatami* Kenrick 1911)—E. Java, Lombok, Lawang, Mauritum, Hatam in Dutch New Guinea.

e. *L. narina neratia* Felder 1864 (= *nahathaka* D'Abrera 1971)—Amboina, Batjan, Obi, Ceram, Halmahera.
f. *L. narina rohini* Marshall 1880 (= *libera* de Niceville 1890, *hybrida* Martin 1896, *tibera* Pagenstecher 1902, *rohina* Mengel 1905)—Assam, E. Burma, Tenasserim, Thailand, Cochin China, Langkawi Islands, Sumatra.
g. *L. narina sangha* Fruhstorfer 1914—Lombok, Sumba.
h. *L. narina sumbawana* Fruhstorfer 1914—Sumbawa.
**4a.** *L. labdaca ancoata* new combination (= *L. ancoata* Grose-Smith 1891, *cinyras ancoata* Fruhstorfer 1898)—NW and SE coastal Madagascar.
b. *L. labdaca labdaca* Westwood 1851 (= *labdaca werneri* Fruhstorfer 1903, *labdaea* Pagenstecher 1911)—equatorial Africa from Sierra Leone to Cameroon, Gabon, Congo, Uganda, W. Kenya, NW Tanzania, Ethiopia, and the Gulf of Guinea islands of Fernando Poo, Principe, and Sao Tome. One old "Honduras" record may be a mislabelling.
**5a.** *L. laius cinyras* new combination (= *L. cinyras* Trimen 1866)—Moka District, Mauritius Island (extinct).
b. *L. laius laius* Trimen 1879 (= *lajus* Pagenstecher 1911, *L. werneri* Hering 1921, *labdaca laius* Swanepoel 1953)—E. coast of Africa from Natal to Kenya; relict on Sao Tome in the Gulf of Guinea.
c. *L. laius lepitoides* new combination (= *L. lepitoides* Moore 1901, *celtis lepitoides* Pagenstecher 1911)—S. extremity of India, Ceylon.
d. *L. laius tsiandava* Grose-Smith 1891—central Madagascar.
6a. *L. myrrha borneensis* Fruhstorfer 1914—Borneo, S. Flores.
b. *L. myrrha carma* Fruhstorfer 1914—SE India.
c. *L. myrrha hecura* Fruhstorfer 1914—W. Malaya.
d. *L. myrrha myrrha* Godart 1819—Java, Bali, Lombok, Sumbawa, Sumba.
e. *L. myrrha myrrhina* Fruhstorfer 1909/10—west-central Sumatra, Sultanate of Deli (island off NW coast of Java).
f. *L. myrrha rama* Moore 1872—SW tip of India, west-central Ceylon.
g. *L. myrrha sanguinalis* Fruhstorfer 1898 (= *L. sanguinalis* Mengel 1905)—Himalayas, west central India, Kashmir, Kulu, Sikkim, Bhutan, Assam, Burma, Tenasserim, Yunnan, Indo-China, Formosa.
h. *L. myrrha thira* Fruhstorfer 1914—Yunnan, Tonkin, Hainan.
i. *L. myrrha yawa* Fruhstorfer 1914—E. Java, Bali.
7a. *L. celtis amamiana* Shirozu 1956—Japan (Amami-Oshima).
b. *L. celtis celtis* Fuessly 1782 (= *celtis ochracea* Milliere 1879, and other named aberrants)—S. Europe, N. Coast Algeria, Asia Minor, Caucasus, Afghanistan, Crimea, Central Asia, India (Chitral State), and the Mediterranean islands of Corsica, Sardinia, Cyprus, Sicily, Tyrrhenian Islands.
c. *L. celtis celtoides* Fruhstorfer 1909 (= *celtis matsumurae* Fruhstorfer 1909)—Korea, Okinawa, Tsushima, Yakushima, Japan (Hokkaido, Honshu, Shikoku, Kyushu).
d. *L. celtis chinensis* Fruhstorfer 1909—west and central China.
e. *L. celtis formosana* Fruhstorfer 1909—Formosa, and Ishigaki and Iriomote (Ryukyu Islands).
f. *L. celtis lepita* Moore 1857 (= *celtis conjuncta* Schawerda 1924)—central Ceylon, S. tip India, Bombay, N. Pakistan, Kashmir, Himalayas, Kumaon, Nepal, Sikkim, Tibet, Upper Burma, Assam, Thailand.
g. *L. celtis sophene* Fruhstorfer 1914—Mekong, Tibet.

B. Genus *Libytheana* Michener 1943 (type = *L. bachmanii* Kirtland 1851).

8a. *L. carinenta carinenta* Cramer 1779 (= *carinata* Burmeister 1878, *carineuta* Kirby 1896)—South America to 35° S. Lat.

b. *L. carinenta mexicana* Michener 1943—Mexico (except Baja) and Central America.

9. *L. terena* Godart 1819 (= *motya* Huebner [in part] 1823, *carinenta terena* Fruhstorfer 1898)—Jamaica, Hispaniola, Puerto Rico, and Para, Brazil.

10a. *L. bachmanii bachmanii* Kirtland 1851 (= *bachmani* Saunders 1868, *carinenta bachmanni* Fruhstorfer 1898, *bachmannii* Klots 1951)—eastern United States and Ontario, Canada. Cuban records for Havana Prov.

b. *L. bachmanii larvata* Strecker 1877 (= *carinenta larvata* Mengel 1905)—Texas (west of Dallas-Houston, to S. California, Baja, and Mexico N. of the Trans-Mexican Volcanic Axis.

11. *L. motya* Huebner 1823 (= *terena* Herrich-Schaffer 1864, *carinenta motya* Fruhstorfer 1898)—Cuba, Guatemala (one record); Brownsville, Texas; Isle of Pines, Hispaniola (Santo Domingo), and Puerto Rico.

12. *L. fulvescens* Lathy 1904 (= *carinenta fulvescens* Pagenstecher 1911)—Dominica (Lesser Antilles).

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## Book Review

*Ecological Studies of Six Endangered Butterflies (Lepidoptera, Lycaenidae): Island Biogeography, Patch Dynamics, and the Design of Habitat Preserves.*
Arnold, Richard A., University of California Publications in Entomology Vol. 99. 1983. 161 pages, paperback.

This most recent University of California Publication in Entomology has as its goal the gathering of "information on the population biologies of. . .six endangered species of butterflies: *Callophrys mossi bayensis* Brown, *Plebejus icarioides missionensis* Hovanitz, *Lycaeides argyrognomon lotis* (Linter), *Euphilotes enoptes smithi* (Mattoni), *E. battoides allyni* (Shields), and *Apodemia mormo langei* Comstock." Richard Arnold clearly succeeds for five of the six species—*L. argyrognomon lotis* proved to be so rare that data were unobtainable. He determines larval host plants and nectar sources, delineates habitat boundaries and calculates a variety of population parameters from mark-recapture studies (the latter valuable in itself since lycaenids have been largely ignored by population biologists using butterflies as their study systems). The contribution of this single monograph goes far in reducing the embarrassingly large lead held by the British in detailed ecological studies of rare and threatened butterflies; a lead resulting from many decades of institution support for research in insect conservation in Great Britain.

This work was not meant, however, to be judged solely on the presentation of autecological results, as the title indicates. Yet beyond the presentation of these data, this monograph disappoints. Rather than a discussion with "broader implications for [the] ecological and evolutionary study of endangered insects in general" (p. 2), we are offered conclusions rehashed from previous authors and an exercise in circular reasoning. For instance, Arnold pursues the idea that the biological characteristics shared by endangered butterflies are those that increase their susceptibility to extinction (p. xii). Superficially this makes a lot of sense. However, this tactic has never generated particularly useful information—e.g., everyone knows top order carnivores are especially extinction-prone, yet that does little to explain why, in East Africa, the cheetah, leopard and wild dog are severely threatened while the lion and hyena are not. Likewise, this methodology tells us nothing new about endangered butterflies and in this study misdirects the entire discussion. Because butterfly numbers appear to be regulated in a density-independent manner in these populations, some of the very characteristics identified as keys to present endangered status (such as sedentary behavior and high host plant specificity—p. 130), are actually characteristics that now contribute to the butterflies' continued survival. Arnold has gone to tiny, isolated habitats and found that the butterflies there don't move much and don't use a wide variety of hosts—hardly a surprising observation.

This is not to suggest that grand counter-intuitive conclusions lurk in a better couched study of endangered butterflies. But lacking an experimental framework, Arnold misses his chance to identify the key biological characteristics of extinction-prone butterflies and to identify the genetic effects of isolation on these surviving populations, if such exist. There are at least three routes to obtain such information. First, one should compare the biologies of a number of butterfly species, both endangered and not endangered, within a single threatened habitat. On San Bruno

Mountain, for example, as yet federally unprotected *Euphydryas editha bayensis* exists in smaller numbers and is probably more threatened with immediate extirpation than either *Plebejus icarioides missionensis* or *Callophrys mossi bayensis*. Likely this is because *E. editha* is not only sedentary and host specific, but its larval hosts are ephemeral annual plants subject to frequent local disappearance due to drought. Furthermore, on San Bruno Mountain in its present state, it may well be widely dispersing butterflies such as some Satyrines and skippers that are truly the most threatened or, for that matter, may be gone already. (Dempster has discussed just such a situation for *Papilio machaon* in small, isolated habitat remnants in Great Britain.)

Second, by comparing endangered subspecies or groups of populations with those that are not endangered, *within the same species*, the characteristics leading to extinction susceptibility may be identified. The five "endangered butterflies" of this study are all simply isolated populations of widespread butterfly species. It is valuable, therefore, to ask how *P. icarioides missionensis* differs biologically from "more successful" populations of *P. icarioides* in, say, the Sierra Nevada or the Great Basin. (Likely very little, but perhaps *missionensis* has lower egg production or poor synchrony with its hosts.)

Third, electrophoretic analysis should be applied in the same contexts: 1) to samples of an array of species from an isolated habitat and 2) to endangered and non-endangered populations of the same species. This is not a criticism, since electrophoresis is expensive, but application of this technique would establish, at the very least, the level of taxonomic differentiation of these endangered populations and, importantly, might show the effects of isolation and small population size on genetic variability. Electrophoresis could also clear up the misuse of the term "ecotypes" (p. 48) for the spatially and temporally overlapping subpopulations of *P. icarioides missionensis*. The discussion of "genetic factors" in management and conservation of these butterflies (p. 143-146) then might be substantive rather than totally hypothetical.

In essence, the results of mark-recapture studies, no matter how rigorous, and natural history investigations, no matter how detailed, by themselves tell us virtually nothing at all about extinction vulnerability in butterflies. The endangered status of these butterflies, in fact, may have nothing to do with biology directly, save their unfortunate co-occurrence with a burgeoning human population in coastal California. When Arnold makes the point, again echoing a host of uncited others, that "the most important attribute of these butterflies is that they serve as *indicators of endangered habitats*" (p. 152), the problem is not that this premise is an old one, but that it is empty; his own data do not support the statement.

One should not confuse the great utility of entire butterfly communities as indicators of habitat status with the importance of one or even a few species. For example, I would argue that the best-studied of the five subspecies, *P. icarioides missionensis*, is a lousy indicator of the overall environmental health of San Bruno Mountain—its populations actually increase in response to the very disturbances that threaten the mountain's ecosystem (pp. 47, 137). Today, the important attribute of *missionensis* on San Bruno Mountain is purely political; that is, its presence on the federal endangered species list. Through this status this blue butterfly has become a tool (arguably not a particularly well-suited one) by which solutions are being fashioned to deal with human sociodemographic problems.

Hence the key common attribute of this collection of lycaenids is that they have been assigned special political status, not that they have inherently unique biological traits.

Exactly how, then, does one apply Arnold's mass of data as "a framework for the design of nature preserves" (p. xii)? Other than monitoring populations for ten to fifteen years (p. 152), setting aside entire existing habitats, renovating them to original forms and functions, and protecting them in perpetuity, no formula is offered at all. Of course, long term study and wholesale preservation is what every one of us wants. But failing all that, which nearly always will be the case, how does one deal with real world constraints?

Let us say a landowner has 1200 acres, of endangered butterfly habitat, and plans to develop his land. After negotiations with concerned groups, the landowner sets aside 800 acres of habitat for permanent protection, retaining the rest for development. To such a scenario Arnold offers not a shred of guidance for the selection and management of a future reserve. Yet it is the need to deal with such real world problems that brought funding for Arnold's study from federal, state, and private agencies. Increasingly, biologists are being offered mediating roles in such conflicts (often the only influence we have in land use decisions). To state that we need a decade to study a given situation clearly misrepresents our ability to engineer economically practical and ecologically responsible management schemes.

In a world where "land is increasingly being drastically altered or converted into urban, agricultural, and industrial sprawl" (p. 1), it is an abdication of responsibility to offer the controlling forces a mass of data sandwiched within a philosophical homily. The conclusions of this study are tantamount to saying these butterflies are endangered because they are "endangered species". Indeed, we would all benefit if Arnold had offered us something novel since we are having an increasingly difficult time coexisting with our butterflies. As this study indicates, on San Bruno Mountain, on the Antioch Dunes, and on the California coastline, the time left to come up with solutions to the problem is running out.

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# THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

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**Manuscript Format: Two** copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

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**COVER ILLUSTRATION: Three "wingless" *Tatochila sterodice* pupae. Photography by S. W. Woo. See Shapiro note, page 262.**

ACKNOWLEDGMENT: We are honored to acknowledge Gerhard Richter of Hanau, West Germany, who provided his expertise in producing the color plate in this issue. Herr Richter, himself a lepidopterist, has kindly agreed to do our color work in the future. His work is clearly of the highest possible calibre, and can otherwise be found in recent issues of the *Nachrichten entomologischen Vereins Apollo*, Frankfurt am Main, Klaus Schurian, editor.