

A NEW HIGH ALTITUDE SPECIES OF *BOLORIA* FROM  
SOUTHWESTERN COLORADO (NYMPHALIDAE), WITH  
A DISCUSSION OF PHENETICS AND  
HIERARCHICAL DECISIONS

LAWRENCE F. GALL<sup>1</sup>

Department of Biology, and Entomology Section Peabody Museum of Natural History,  
Yale University, New Haven, Connecticut, USA 06511

AND

FELIX A. H. SPERLING

Department of Zoology, University of Alberta,  
Edmonton, Alberta T6G 2E9, Canada

**ABSTRACT.** A new *Boloria* was collected for the first time in July 1978 on Mt. Uncompahgre in southwestern Colorado. It is described as a full species, *B. acrocnema*, most closely related to *B. improba* whose southern limit is more than 1800 km to the north. Adult characters, including genitalia, wing-pattern and venation, and ultraviolet reflectance patterns, are analyzed numerically. Classical and numerical taxonomic approaches to this situation are contrasted, and the utility of phenetics in hierarchical decisions is discussed. A practical guide to specimen recognition, and some aspects of the distribution and ecology of the butterfly are also presented.

Butterfly systematists lately have recognized a number of phenotypically cryptic species after closer examination of already amassed material (e.g., Stallings & Turner, 1954; Burns, 1960; Remington, 1968; Cardé, Shapiro, & Clench, 1970; Clench, 1972), and it is likely that many more distinct species remain undetected in the major collections. New and previously uncollected butterfly species, in contrast, are rarely being discovered in temperate North America. *Sandia macfarlandi* (Ehrlich & Clench, 1960) is the most prominent recent discovery of this kind.

On 30 July 1978 a party of five from the Rocky Mountain Biological Laboratory (including Scott M. Graham, Kathleen A. Shaw, Wendy E. Roberts, and the authors) discovered a colony of a hitherto unknown *Boloria* some 600 to 700 m above timberline on Mt. Uncompahgre, Hinsdale County, Colorado. In general appearance the Uncompahgre specimens are most similar to specimens of the circumpolar butterfly *B. improba* (Butler), but they possess an array of different phenotypic characteristics. We have concluded that this taxon represents a distinct species, for reasons discussed in detail below, and it is described as new, as follows.

---

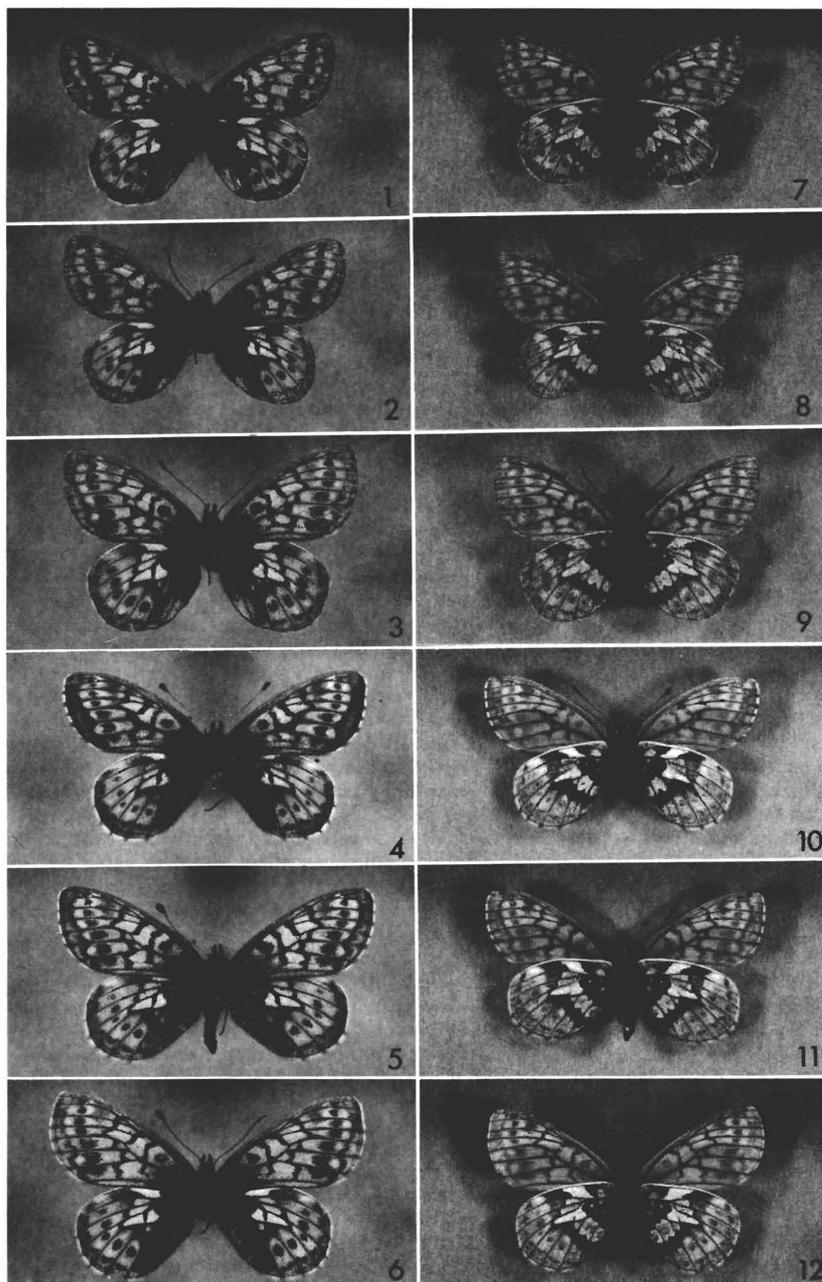
<sup>1</sup> This author and Biology Department address for reprint requests.

***Boloria (Clossiana) acrocne* Gall & Sperling, new species**

**Description.** **Male** (Figs. 1-6). **Head:** eyes dark brownish black; clypeal and vertex hairs rust brown; mean length of antenna 7.8 mm (range = 7.4-8.4; holotype 7.9. This format is followed throughout species description; sample numbers as in Characteristics section), shaft light brownish black, checkered with white, club black with orange terminus; labial palps clothed with black and rust brown hairs. **Thorax:** clothed dorsally with rust brown hairs, white hairs interspersed posteriorly; femora covered with long rust brown hairs, tibiae and tarsi with shorter light brown hairs. **Abdomen:** deep brownish black, clothed with long rust brown hairs; segments VII-VIII with numerous white hairs ventrally. **Forewing:** mean length 15.8 mm (14.9-17.1; 15.4), width 8.0 mm (7.5-8.5; 7.8); margins distinctly rounded. Dorsal surface: ground color golden brown, variably flushed with white basad of postmedian band; heavy melanization confined to basal area, long white hairs covering this region; outer margin checkered black and white; postmedial, medial, and subbasal bands black, thin, and contrasting sharply with ground color; postmedial band in cells  $M_3$  and  $Cu_1$  closely adjoining discocellular crossveins; veins  $R_2$  to  $R_4$  branching from radial stem near apex; submarginal band extending to inner margin through cell  $Cu_2$ , with a prominent cross bar connecting with postmedial band; rounded spot present in variable position in postbasal section of discal cell; submarginal spots large and oblong, filling one-fourth to one-half of cells, the most caudad spot filling greater than or equal to one-half of its cell and joined to marginal band. Ventral surface: ground color light golden brown, flushed marginally with reddish brown; veins and bands brownish black to black, contrasting with ground color. **Hindwing:** mean length 12.0 mm (11.4-12.5; 11.5), width 8.9 mm (8.2-9.8; 9.0), margins distinctly rounded. Dorsal surface: ground color golden brown, often flushed with white in discal area; heavy melanization confined to basal area and anal margin below disc; outer margins checkered black and white; conspicuous D-shaped whitish or golden patch in basal section of discal cell; maculation black, contrasting with ground color. Ventral surface: discal ground color deep cinnamon-brown, contrasting with golden brown limbal area; submedian-median row complete, heavily flushed with silvery-white, indented sharply at junction of discal cell and cells  $Cu_1/Cu_2$ ; submedian-median row thin below discal cell, directed toward anal angle; several white basal spots present. **Male genitalia:** uncus horn-shaped, mean length 0.40 mm (0.38-0.43; 0.40), lateral processes diverging perpendicularly; caudal section of tegumen heavily sclerotized, diverging cephalad slightly from the center; inner face of valve covered with numerous small setae, mean length of valve 1.63 mm (1.56-1.68; 1.62); cucullus stout, covered with long setae, a single thick prong projecting inward at terminus; digitus slender, mean length 0.43 mm (0.38-0.47; 0.46), distal end slightly distended and covered with small spines; juxta U-shaped, dorsal projections bilobed; mean length of aedeagus 1.42 mm (1.37-1.55; 1.52), distal half slender with a single long rostellum, proximal half slightly distended; caecum short and blunt.

**Female** (Figs. 7-12). **Head:** as in male, but palps browner; mean length of antenna 8.2 mm (7.7-8.6; allotype 8.0). **Thorax:** as in male. **Abdomen:** as in male, but with white hairs confined to immediate area of genital opening. **Forewing:** maculation patterns and coloration as in male with the following exceptions: connecting bar in cell  $Cu_1$  variably expressed, submarginal spots extending over smaller area in their cells, the most caudad spot occasionally joined to marginal band. **Hindwing:** as in male. **Female genitalia:** lamella postvaginalis a finely sculptured funnel, open and membranous at distal end; lamella antevaginalis with wide semicircular lobes projecting ventrad; posterior section of genital plate forming two semicircular plates articulating laterally, their ventral margins covered with soft hairs; papillis analis soft, sparsely covered with short hairs, apophysis posterioris short; sternum VII forming thin rectangular plate over lamellae and ductus bursae; entire genitalia lightly sclerotized.

**Type series.** All specimens of *B. acrocne* captured in 1978 have been designated as primary types or paratypes. Locality data for each is as follows: taken 30 July 1978 on Mt. Uncompahgre, 13.0 km NW of Lake City, Hinsdale Co., Colorado, elev. 4080-4140 m. The Holotype ♂, Allotype ♀, and 18 paratypes (12 ♂, 6 ♀) have been placed



FIGS. 1-12. Specimens of *Boloria acrocnema*, new species. Figs. 1-6. Dorsal surfaces: 1-3, males (1, Holotype); 4-6, females (4, Allotype). Figs. 7-12. Undersurfaces of same specimens in Figs. 1-6. All specimens taken 30 July 1978, Mt. Uncompahgre, Hinsdale Co., Colorado, elev. 4080-4140 m, leg. L. F. Gall & F. A. H. Sperling.

TABLE 1. Characters most readily used when separating specimens of *B. acrocnemata* and *B. improba*. Full descriptions of the characters are given in the text. See also Figures 13–24.

Character	<i>B. acrocnemata</i>	<i>B. improba</i>
1. FW radial veins R <sub>2</sub> –R <sub>4</sub>	branching near apex	branching further down radial stem
2. Dorsal melanization	confined basally	extensive
3. Overall maculation	thin; contrasting with ground coloration	wide; blurred
4. Postmedial DFW band	offset; close to crossveins in M <sub>3</sub> and Cu <sub>1</sub>	more connected; further margined
5. DHW discal cell spot	clear, crisp	obscured
6. VHW submedian-median row	complete; silvery-white; strongly indented basally	absent to complete, duller yellow; not indented
7. Uncus and tegumen processes	T-shaped	Y-shaped
8. Valve length	1.54–1.66 mm (mean = 1.63 mm)	1.78–2.06 mm (mean = 1.92 mm)

in the Peabody Museum of Natural History, Yale University. Three paratypes (2 ♂, ♀) have been placed in the Canadian National Collection, Ottawa, four (2 ♂, 2 ♀) in the American Museum of Natural History, New York, and another 14 (8 ♂, 6 ♀) have been retained in the personal collections of Kathleen A. Shaw and the junior author. Total number in type series 41 (25 ♂, 16 ♀).

**Etymology.** The name is a latinization of the Greek roots *acro* (the top of) and *cnemus* (the mountain slope), descriptive of the type locality. The adjectival specific name, which conforms in gender to the feminine *Boloria*, may be pronounced either ä-krō-NĒ-ma or ä-krō-KNĒ-ma. We suggest the Uncompahgre Fritillary as a common name.

**Remarks. Characteristics of *B. acrocnemata* compared to those of *B. improba*.** The most useful characters distinguishing *B. acrocnemata* from other *Boloria*, especially *B. improba*, are described below and in Table 1, and are shown in Figs. 13–24. 117 specimens have been examined for wing-pattern and venation characteristics: 20 ♂, 11 ♀ *B. acrocnemata*; 15 ♂, 21 ♀ *B. i. improba* (Butler); 19 ♂, 17 ♀ *B. i. youngi* (Holland); 9 ♂, 5 ♀ *B. i. improbula* (Bryk); for male genitalia: 10, 6, 16, and 4, respectively. We hereafter use specific localities, and the general geographic terms North American arctic, Canadian subarctic (=western Hudsonian and northeastern Montanian biotic provinces of Dice, 1943; see also Freeman, 1956), and Scandinavian arctic, respectively, in reference to the *B. improba* populations analyzed. Unless otherwise indicated, *B. improba* refers to the specimens from all geographic areas. Metric data are arithmetic means in millimeters; most were taken from the phenetic analyses.<sup>2</sup>

<sup>2</sup> Differences in character distributions between *B. acrocnemata* and, in each case, the most similar geographic sample of *B. improba* are all significant at the 0.05 level (all but two at the 0.01 level, these distributions being essentially non-overlapping in range). Those among the *B. improba* samples, except the ratio of digitus length to valve length (roughly, North American arctic > Canadian subarctic = Scandinavian arctic at the 0.05 level) are insignificant ( $p > 0.10$ ; Mann-Whitney U-tests, degrees of freedom vary according to sample comparisons). Metric data for Albatross specimens of *B. improba* have been lumped with those from other Canadian subarctic localities for analysis (due to small sample size: 3 ♂, 3 ♀), although this population has been discussed separately on occasion in the text. Female Scandinavian arctic *B. improba* have not been numerically analyzed either due to small sample size. Statistical methods follow Sokal & Rohlf (1969) and Rohlf & Sokal (1969).

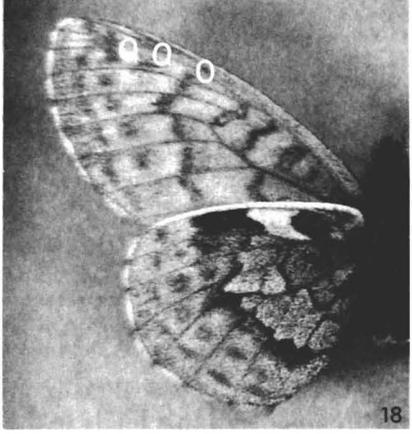
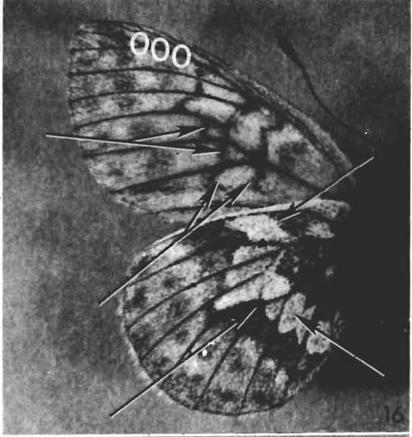
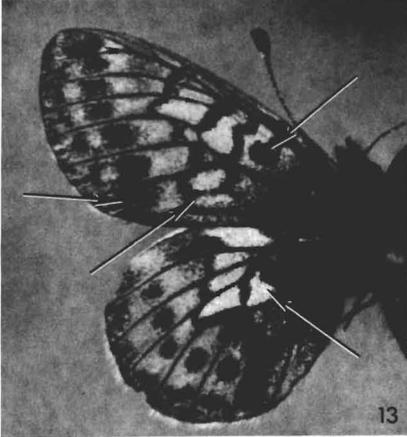
Table 1 gives a synopsis of those characters we find most expedient when sorting pinned specimens. These and other differences are discussed in greater detail here. The dorsal maculation patterns in *B. acrocneuma* are sharp, contrasting with the ground coloration (cf. normally very blurred in *B. improba*), and the vertical dashes comprising the medial and postmedial forewing bands are thinner and less colinear than in *B. improba*. The postmedian forewing band in cells  $M_3$  and  $Cu_1$  is located much closer to the discocellular crossveins in *B. acrocneuma*. The submedial forewing band extends directly through cell  $Cu_2$  to the outer margin, usually with a thick bar extending distad to the postmedian band; the former character is located further basad in *B. improba*, the distance between the bands being greater (most visible on ventral forewing surface). Specimens of *B. acrocneuma* exhibit a prominent, free-standing basal forewing spot, whereas in virtually all *B. improba* this same spot is squarer and broadly connected to the costal and cubital stem. The most caudad spot of the forewing submarginal band is large and broadly connected to the marginal band in *B. acrocneuma*, but is smaller and free-standing in *B. improba*. Heavy melanization extends across much of the forewing basal area and 50–75% of the hindwing in *B. improba*, especially in material from the District of Franklin, Canada, but is quite restricted in *B. acrocneuma*. The D-shaped patch in the basal section of the hindwing discal cell is crisply delimited in *B. acrocneuma*, but obscured in *B. improba* (sometimes totally absent in North American arctic material).

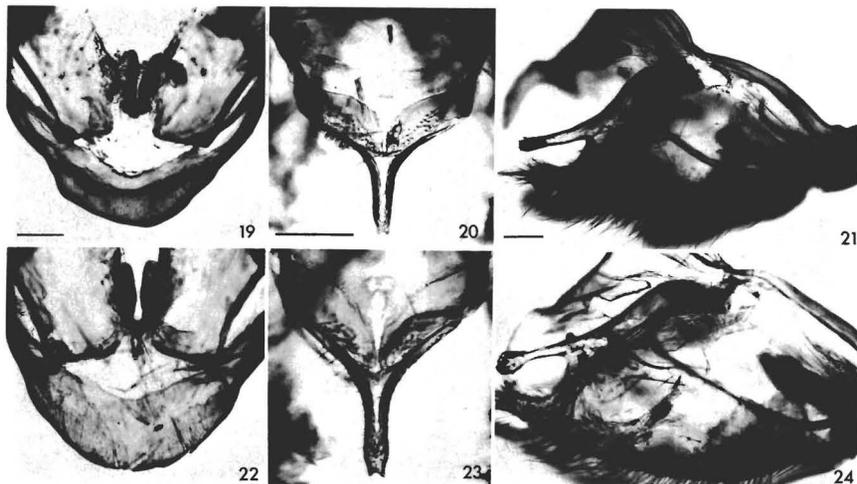
The forewing veins  $R_4$ ,  $R_3$ , and especially  $R_2$  are all shorter in *B. acrocneuma* (males: 2.98, 4.04, 5.15; females: 3.28, 4.38, 5.68) than in North American arctic (3.42, 4.97, 6.41; 3.76, 5.52, 7.03), Canadian subarctic (3.58, 5.12, 6.68; 3.85, 5.56, 7.23), and Scandinavian arctic (3.67, 5.23, 6.43) *B. improba*. These veins thereby appear compressed near the apex in *B. acrocneuma*. The white circles in Figs. 13–18 indicate their branch points from the radial stem. In addition, the length-to-width ratios of fore- and hindwings of *B. acrocneuma* (1.97, 1.31; 1.96, 1.29) are slightly greater than in North American arctic (1.89, 1.19; 1.88, 1.21), Canadian subarctic (1.87, 1.21; 1.87, 1.21), and Scandinavian arctic (1.88, 1.22) *B. improba*. The marginal wing angles are also distinctly rounded in *B. acrocneuma*, and when coupled with the ratio characters, they give its wings an oblong appearance.

Ventrally in *B. acrocneuma* the well-defined submedian-median row is complete, heavily flushed with silvery-white, and contrasts strongly with the surrounding ground coloration (deep cinnamon-brown). This row is incomplete in North American arctic *B. improba* (often entirely absent in material from the Northwest Territories of Canada) and more complete in Canadian subarctic material, but is wider, duller yellow, and less contrasting with the ground coloration (yellow- to orange-brown). In Scandinavian arctic *B. improba* the row is sometimes complete, but is not as contrasting or heavily flushed with silvery-white. In *B. acrocneuma* this row is also conspicuously indented basally near the junction of cells  $Cu_1/Cu_2$  and the discal cell, and is directed toward the anal angle. In *B. improba* the band is not indented and is directed more toward the inner margin. The most cephalad spot of the submedian-median row (white costal

→

FIGS. 13–18. Comparison of wing-pattern characteristics of *Boloria acrocneuma* to those of *Boloria improba*. Arrows and white circles indicate several of the characters discussed in the text. **13**, upper surface of male holotype, *B. acrocneuma*; locality data as before. **14**, upper surface of a male *B. i. youngi*; taken 7 July 1975, Pink Mountain, 135 km NW of Ft. St. John, British Columbia, elev. 1820 m, leg. G. J. Hilchie. **15**, upper surface of a male *B. i. improba*; taken 17 July 1952, Chandler Lake, Brooks Range, Alaska, leg. G. W. Rawson. Figs. **16–18**, undersurfaces of same specimens in Figs. 13–15. These specimens correspond to ACR-CO 3, IMP-BC 2, and IMP-AK 3 on the phenograms (see Figs. 28–30). Note the right-left asymmetry in pattern of forewing basal spot in holotype of *B. acrocneuma* (cf. Fig. 1).





FIGS. 19–24. Representative genitalic differences between *Boloria acrocneuma* and *Boloria improba*. Figs. 19–21. Paratype of *B. acrocneuma*: 19, ventral view showing width of saccus; 20, cephalic view showing length of uncus and shape of uncal/tegumen processes; 21, lateral view showing length of valve, and associated structures. Figs. 22–24. Same characters from a specimen of *B. i. youngi*, figured as representative for the species. Locality data as before. Each pair of photographs taken at the same magnification; scale bars are 0.25 mm.

spot) is thin and strongly concave basally in virtually all *B. improba* but is wider and straight in *B. acrocneuma*.

In the male genitalia of *B. acrocneuma* the more heavily sclerotized caudal sections of the tegumen diverge cephalad from the center only slightly, as do the lateral processes of the uncus, the combination appearing T-shaped when viewed dorsally (Fig. 20). These same structures diverge considerably and appear Y-shaped in *B. improba* (Fig. 23). The uncus length, valve length, and saccus width are all smaller in *B. acrocneuma* (0.40, 1.63, 0.79) than in North American arctic (0.47, 1.92, 0.98), Canadian subarctic (0.50, 1.94, 1.10), and Scandinavian arctic (0.47, 1.90, 0.98) *B. improba* (see Figs. 19–24). Indeed, the entire genitalia of *B. acrocneuma* are noticeably smaller than in *B. improba*. There are also a number of differences in proportion; for example, the ratio of digitus length to valve length is greater in *B. acrocneuma* (0.27) than in North American arctic (0.23), Scandinavian arctic (0.21), Albertan (0.18), and other Canadian subarctic (0.21) *B. improba*.

Although generally similar to the visible facies pattern, the ultraviolet reflectance pattern of the ventral surface of *B. acrocneuma* highlights the prominent submedian-median row, which is absent or present only as a trace in Nearctic *B. improba* (Figs. 25–27; characters most noticeable in males). Only the lower half of the discal cell spot appears strongly reflective in *B. improba* (cf. entire cell in *B. acrocneuma*).

The foregoing classical taxonomic comparisons indicate our butterfly is distinct, and this leads to the next question: at what hierarchical position should *B. acrocneuma* be placed? Only *B. acrocneuma* and its phenotypic nearest neighbor, *B. improba*, are treated in detail above.



FIGS. 25-27. Ventral surface ultraviolet reflectance patterns of *Boloria acrocneema* and *Boloria improba*. **25**, *B. acrocneema*; **26**, *B. i. youngi*; **27**, *B. i. improba*. Males in upper row, females in lower row of each figure. Taken with PAN-X film and standard Wratten filter. Characters discussed in text.

Although customary when new taxa are erected, such one-to-one morphometric comparisons often do not adequately address questions of rank (e.g., species or very distinct subspecies?). The present situation involves phenotypically discrete populations in extreme allopatry, which of course prohibits analysis of sympatric interactions, the most useful test of biological distinctness. Hybridization experiments have not yet been undertaken to measure genetic incompatibilities, and biochemical data are also unavailable. Moreover, the general life his-

tories and ecologies of *B. acrocnema* and *B. improba* are not yet well known. Another method for indexing rank is to compare their phenotypic distinctness with other similar *Boloria*. An argument may be constructed as follows: if the degree of overall phenotypic difference between *B. acrocnema* and *B. improba* is comparable to that between universally accepted, closely related species, then *B. acrocnema* should also be treated as a distinct species. Since *B. frigga* (Thunberg), *B. bellona* (Fabr.), and *B. epithore* (Edw.) are phenotypically close to *B. improba*, and these four species have been associated as members of the subgenus *Clossiana* (e.g., Warren, 1944; dos Passos & Grey, 1945; Klots, 1951; dos Passos, 1964; Higgins & Riley, 1970), we thus use them here for comparison. In addition, analyzing intraspecific variation within each *Boloria* species (e.g., Perkins & Meyer, 1973 for *B. epithore*) provides the necessary further checkpoints for correlating relative phenotypic differences with differing levels of accepted taxonomic affinity.

Phenotypic variability within and between populations can be great in *Boloria*, and this is especially noticeable in series of *B. improba*. While single- and few-character schemes are sometimes useful in taxonomic inquiry, these methods normally are unable to cope with extensive variability (e.g., Lafontaine, 1970; see Gall, 1976) and cannot give reliable estimates of overall similarity. Accordingly we are employing some of the multivariate techniques of numerical taxonomy in the following investigation.

#### TAXONOMIC RANK: PHENETIC METHODS

We present a brief overview of our objectives and methods in this work. The next few paragraphs are a partial, non-technical summary of both. Numerical taxonomy encompasses diverse techniques for exploring phenotypic and phyletic relationships. The field grew rapidly with the advent of digital computers in the 1960's, and several sub-disciplines have since emerged, most notably cladistics and phenetics. We present some of the techniques and philosophy of the latter.

The methods of phenetics are shared by several fields, including systematics, psychology, economics, and ecology. Systematists have typically employed phenetics or phenetic-like methods for large revisionary works or for inferring phyletic patterns among many taxa, although cladistics are now more frequently used for phyletic interpretation. We are not embarked upon such a broad study; rather, we are using phenetics as a tool for attacking a locally defined problem. Roughly, when using phenetics in taxonomy, one attempts to order taxa into groups defined by quantitative measures of similarity or difference. Sneath & Sokal's (1973) book, *Numerical Taxonomy*, is the

basic reference treating numerical taxonomic (esp. phenetic) theory and practice. For other approaches to systematic problems, reviews of species concepts, and bases upon which to establish classifications see: Mayr, 1963, 1974; Hennig, 1966; Michener, 1970; Sokal, 1975; Brothers, 1975; and the journal *Systematic Zoology*.

In numerical taxonomic work one uses many characters simultaneously (anywhere from a few dozen to several hundred). Corollary considerations—among them the effect of character correlation upon the taxonomic pattern—have been posed for techniques such as factor, canonical, and discriminant analysis. We use a kind of factor analysis called principal component analysis, in part since it expedites examination of character correlation and variation in large data sets, and because the method will also faithfully represent phenetic differences among fairly distinct groups (the species and subspecies under comparison; see Rohlf, 1968). For a full discussion of factor analysis and related techniques see Harman (1976). These numerical methods are typically used for detailed descriptions of character-character relationships in large data sets. As an example of another use for principal component analysis, especially for practicing systematists, we screened for various taxonomically discriminating character sets with reference to statistics the computer printed for us (match the relative character weightings given in the Appendix with the positions of the *Boloria* on each principal axis in Fig. 31). Many of the individually diagnostic *acrocnema-improba* characters, and character suites, were first recognized in this manner; a later close inspection of the *Boloria* yielded others.

Before considering the phenetic data, we emphasize two related systematic concerns. Although an old and attractive concept, the possibility of specifying locally (e.g., within *Boloria*) or more globally (e.g., all insect orders) defined standards for measuring hierarchic rank has received relatively little critical attention. Understandably, the necessary prerequisites for such endeavors are synthetic reconciliations of varied species concepts and systematic philosophies. Nevertheless, for many sections of the butterflies, where “splitting” and “lumping” are often practiced simultaneously by different authors, more standardized quantitative approaches (however defined for the present) seem particularly valuable to us. Secondly, classifications and systematic decisions arrived at via phenetic, cladistic, and classical taxonomic techniques tend to converge, especially at lower taxonomic levels. This convergence follows because classical taxonomists have long performed a sort of numerical taxonomy in their heads, perhaps best termed pattern recognition in the broad sense. The convergence holds only to a certain extent. Some groups consis-

tently defy adequate taxonomic structuring *sensu lato* (in the Lepidoptera: *Euphydryas*, *Colias*, the eastern North American *Hemileuca maia* complex, the *Catocala* [although species boundaries do not seem as much at issue here], and many lycaenid groups, to name a few), and for these phenetic and cladistic treatment would probably be most illuminating.

### Materials and Methods

From larger series of available male *Boloria*, 4 *B. i. improba*, 6 *B. i. youngi*, 3 *B. i. improbula*, 3 *B. frigga saga* (Staud.), 2 *B. f. sagata* (Barnes & Benj.), 7 *B. bellona bellona*, 2 *B. epithore epithore* (Edw.), 3 *B. e. chermocki* Perkins & Perkins, 3 *B. e. borealis* Perkins, and 7 *B. acrocneuma* were selected for comparative analysis. The genitalia of each were dissected and these individuals scored over an array of 30 genitalic and 45 wing-pattern characteristics. The female analysis involved 4 *B. i. improba*, 4 *B. i. youngi*, 2 *B. i. improbula*, 3 *B. frigga saga*, 3 *B. f. sagata*, 8 *B. bellona bellona*, 2 *B. epithore epithore*, 3 *B. e. chermocki*, 2 *B. e. borealis*, and 6 *B. acrocneuma* scored for 39 wing-pattern characteristics. Some wing-pattern characters were easily scored by eye; others and the genitalic characters were scored using a binocular dissecting microscope with an ocular micrometer. The characters employed are listed in the Appendix. Included in the genitalic analysis with *B. i. youngi* were specimens from Prospect Mountain, Alberta, the southernmost population of this butterfly presently known (Pike, 1978).

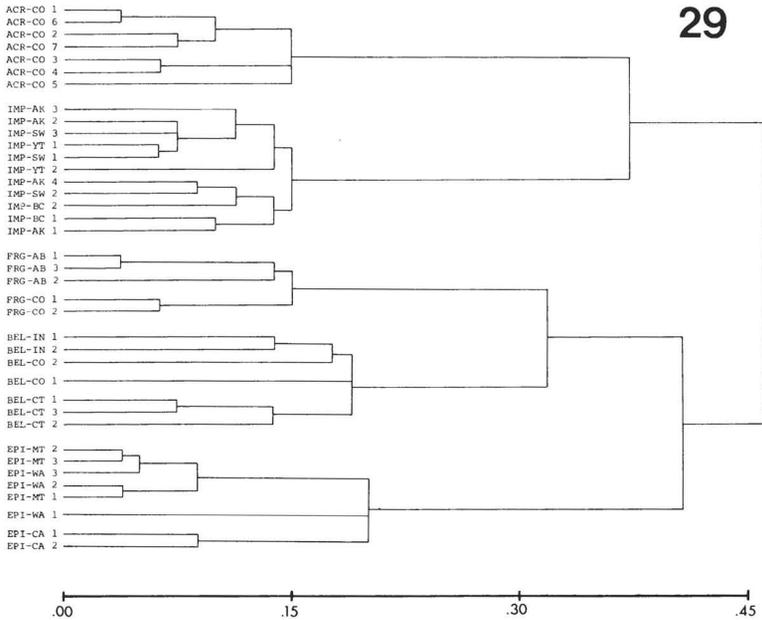
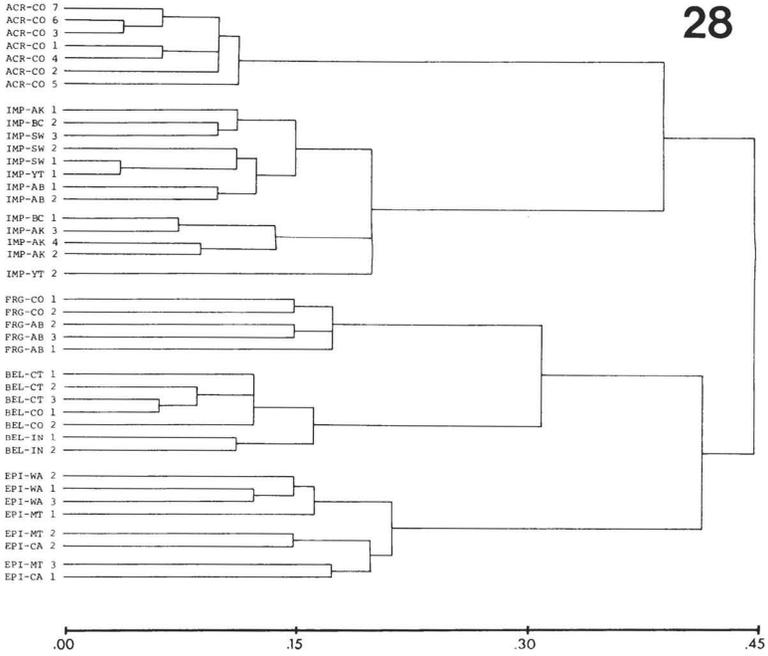
Specimens of *B. i. youngi* and *B. i. improbula* were borrowed from the American Museum of Natural History. Additional *B. i. youngi* were drawn from the personal collections of G. J. Hilchie, E. M. Pike, and the junior author. Uncompahgre material was drawn from both authors' collections, and all others from the entomological collections at the Peabody Museum of Natural History, Yale University. Locality data for the sample specimens other than *B. acrocneuma* are as follows: *B. i. improba*: Chandler Lake and vicinity, and Umiat, Alaska; Baker Lake and Chesterfield, Northwest Territories. *B. i. youngi*: Pink Mountain and Atlin, British Columbia; nr. International border on Alaska Highway, Yukon Territory; Prospect Mountain, Alberta. *B. i. improbula*: Abisko and vicinity, Sweden. *B. frigga saga*: Spray Lake region, Alberta; Riding Mountain, Manitoba. *B. f. sagata*: Gothic and vicinity, Colorado. *B. bellona bellona*: New Haven, Fairfield, and Litchfield Counties, Connecticut; nr. Somerset, Colorado; Burlington and vicinity, Indiana. *B. epithore epithore*: Santa Cruz Mtns., California. *B. e. chermocki*: Salmon Meadows, Okanogan County, Washington. *B. e. borealis*: Mission Mtns., Montana.

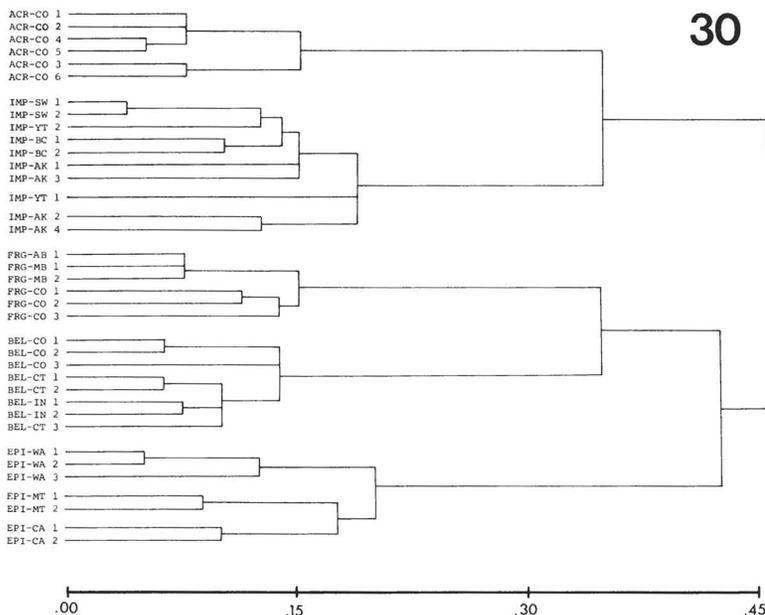
At higher taxonomic levels or when highly discrete characters are most plentiful, an "exemplar" approach in numerical taxonomic studies is often feasible (one individual chosen as representative of a taxon, usually species; see Ehrlich & Ehrlich [1967] for an exemplar treatment of world-wide butterfly relationships). Since our taxa exhibit moderate phenotypic variability, we have chosen a level intermediate between the exemplar approach and exhaustive, and costly, analysis of many individuals. Sections of Parks' (1970) FORTRAN IV numerical taxonomy program and others written by the senior author were combined and modified for use on the Yale University Computer Center IBM System/370 computer. This composite program performs the following operations: a) normalization of input character vectors; b) principal component analysis of character variation; c) transformation of original characters to normalized component scores for each specimen; d) construction of a similarity matrix using these component scores and the simple Euclidean distance function (Parks, 1968); e) unweighted pair-group cluster analysis of specimens, again using the distance function. The program then prints a branching tree of phenetic distances (phenogram) in addition to intermediate principal component and cluster analysis parameters. Other options exist, but were not used here. All runs utilized a series of preset default control values during principal components extraction (e.g., minimum of five axes extracted; see Parks, 1970). Varying these conditions (notably, the extraction of additional axes—up to eight in one case) did not alter the basic taxonomic decisions presented below.

#### Results of Phenetic Analyses

Phenograms of the male genitalic, male wing-pattern, and female wing-pattern relationships were redrawn from the computer output and are shown in Figs. 28–30, respectively. Clusters of *Boloria* separated by more than 35–40% of the maximum distance encountered have been double-spaced for emphasis. A phenogram conveys one-dimensional information; in this case only the horizontal distances have meaning (i.e., all cluster pairs are rotationally symmetric about their higher [right-hand] stems). Distances between specimens are calculated from the origin to the vertical bar connecting them.

In each analysis *B. acrocneuma* is readily separable from the others and is phenetically closest to *B. improba*. All described *Boloria* species are readily distinguishable by both wing-pattern and genitalia. Intraspecific variation is diverse, and most ill-defined in *B. improba*. The recognized subspecies of *B. improba* show only weak tendencies to separate on genitalia or wing-pattern characters. Using classical taxonomic methods, Brunn & von Schantz (1948) had pre-





FIGS. 28–30. Phenograms of *Boloria* relationships. **28**, male genitalic phenogram, cophenetic correlation coefficient CPCC = 0.851; **29**, male wing-pattern phenogram, CPCC = 0.877; **30**, female wing-pattern phenogram, CPCC = 0.830. Individuals designated by a three letter acronym, an individual sample number, and a two letter geographic identifier (AB = Alberta; AK = northern Alaska and Northwest Territories; BC = British Columbia; CA = California; CO = Colorado; CT = Connecticut; IN = Indiana; MB = Manitoba; MT = Montana; SW = Sweden; WA = Washington; YT = Yukon Territory). Value of Euclidean distance coefficient,  $d$ , given below each phenogram. Note the position change of individual males within, but not between, major clusters in the genitalic and wing-pattern phenograms.

viously found no “constant difference” between the genitalia of Scandinavian and northern Alaskan *B. improba*. The two subspecies of *B. frigga* are readily separable; those of *B. epithore* show variable relationships, with the highly disjunct *B. e. epithore* from coastal California most consistently separated from the others. The widely separated populations of *B. bellona* (not recognized at the subspecific level) are roughly distinguishable, most distinctively on wing-pattern characters.

Phenograms have the advantage of representing multi-dimensional relationships in a single dimension but are consequently subject to problems of distortion. This distortion becomes most apparent at higher level cluster distances, and in many instances can be a serious stumbling block to phyletic extrapolations. Listed in Table 2 are all

TABLE 2. Pairwise interspecific phenetic distances (d) just prior to final clustering. All individual specimens from within classically defined species have since joined. There are 10 possible species-species distances, and 10 possible intraspecific distances. Three intraspecific distances are for widely separated populations of *B. bellona bellona* not formally recognized at the subspecific level.

Species pair	Character set					
	♂ Genitalia		♂ Wing-pattern		♀ Wing-pattern	
	d	rank d	d	rank d	d	rank d
<i>frigga-bellona</i>	0.310	1	0.317	1	0.349	2
<i>frigga-epithore</i>	0.488	8	0.429	4	0.476	8
<i>frigga-acrocnema</i>	0.524	9	0.506	10	0.463	7
<i>frigga-improba</i>	0.464	7	0.432	5	0.447	6
<i>bellona-epithore</i>	0.362	2	0.392	3	0.393	4
<i>bellona-acrocnema</i>	0.556	10	0.465	8	0.401	5
<i>bellona-improba</i>	0.379	3	0.483	9	0.491	9
<i>epithore-acrocnema</i>	0.452	6	0.459	7	0.527	10
<i>epithore-improba</i>	0.396	5	0.439	6	0.386	3
<b><i>acrocnema-improba</i></b>	<b>0.388</b>	<b>4</b>	<b>0.372</b>	<b>2</b>	<b>0.344</b>	<b>1</b>
maximum intraspecific cluster distance	0.201		0.185		0.204	

the possible pairwise species-species phenetic distances, after intraspecific but prior to interspecific clustering (a sort of null hypothesis has been confirmed here: all specimens from within classically defined species have clustered most closely). Reference to the phenograms will indicate the compromises involved during clustering, although in general the unweighted pair-group method tends to conserve phenetic distances i.e., there is no systemic dilation or contraction. Note that the male genitalic and wing-pattern relationships are extremely close, on character suites often considered somewhat divergent in biological process and taxonomic utility.

In order to circumvent the distortion inherent in phenograms, an ordination plot was constructed using the combined sets of male genitalic and wing-pattern characteristics, with the first three principal components extracted as axes (Fig. 31). All 75 characters were used; the Appendix lists the principal component to which each character contributes most heavily. The ordination plot more graphically portrays the distinctness of *B. acrocnema* and the relationships among the various *Boloria*. Since a) *B. acrocnema* is readily distinguishable from its phenotypic nearest neighbor, *B. improba*, b) the phenetic distances between them are comparable to all other species-species distances, and greater than some, and c) these distances are much greater than all intraspecific linkages, we have accorded our Uncompahgre *Boloria* full species status.

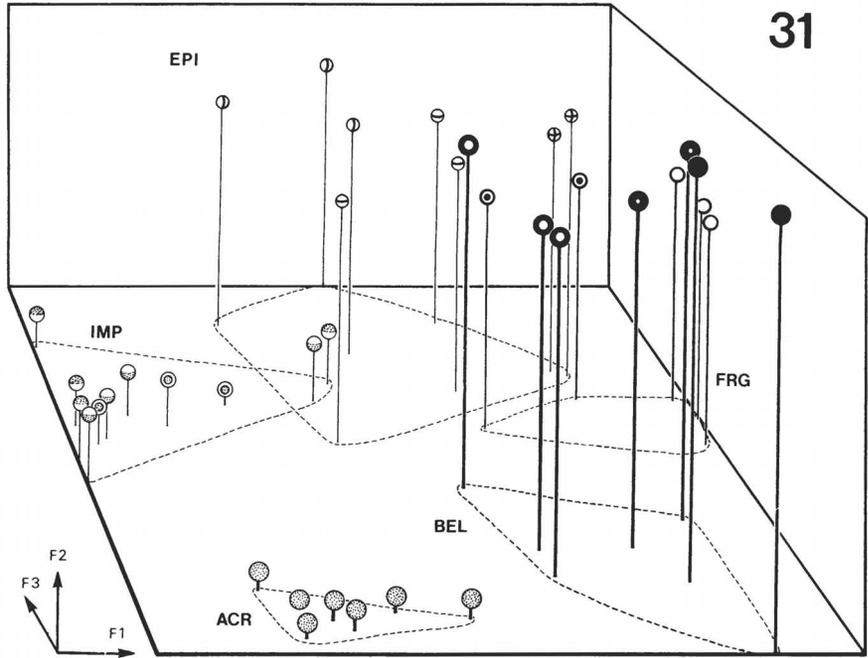


FIG. 31. Ordination plot of male *Boloria* phenetics prepared from 75 genitalic and wing-pattern characters. Black circles, *B. bellona bellona* (filled, Indiana; small open circle, Colorado; large open circle, Connecticut). Striped circles, *B. epithore* (vertical, *chermocki*; horizontal, *borealis*; cross, *epithore*). Half-stippled circles, *B. improba* (upper-filled, *improba*; lower-filled, *youngi*; center-filled, *improbula*). Open circles, *B. frigga saga*; black center, *B. frigga sagata*. Stippled circles, *B. acrocneuma*. Principal component axes indicated at lower left. Note the distinctness of species hypervolumes and semi-random assortment of subspecies within these regions.

## DISCUSSION

Much slighter phenotypic differentiation over shorter geographic distances than shown by the *acrocneuma-improba* pair often conceals extensive genetic divergence (e.g., Kruckeberg, 1957; Moore, 1967; Oliver, 1972, 1977; see Ayala, 1975, and White, 1978, for reviews of genetic differentiation during speciation). It is notable that Oliver (op. cit.) found considerable genetic incompatibility between geographically separated yet "phenotypically indistinguishable" populations in both *B. bellona* and *B. selene* (Schiff.) from the Nearctic region. We predict concomitant genetic differences will be found between *B. acrocneuma* and *B. improba* when the appropriate biochemical and crossing analyses are conducted. We also draw attention to discordance in geographical trends among the various characters studied,

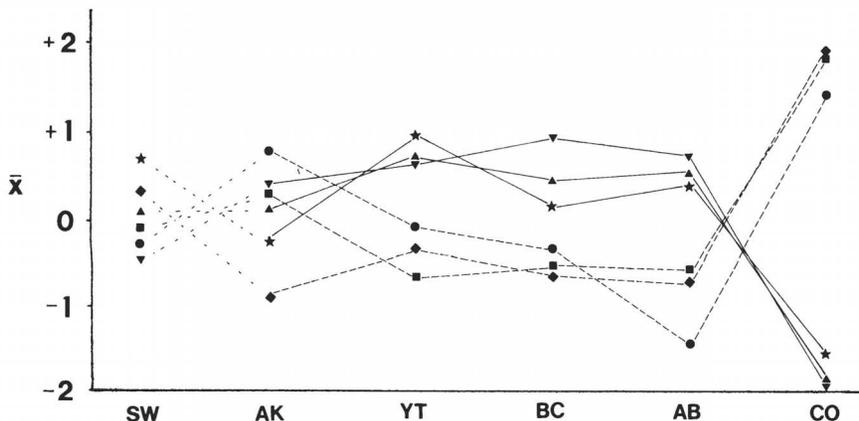


FIG. 32. Trends in means of six metric characters across the combined geographic ranges of *B. improba* (SW to AB) and *B. acrocneuma* (CO). Locality abbreviations as before, except here AK refers only to northern Alaskan material. Characters 9, 12, 25, 52,  $R_4$ , and hindwing length to width ratio represented by circle, downward triangle, upward triangle, square, star, and diamond, respectively. Standardization is for graphical comparability only; see text for statistical analyses. Although discordance is extensive, note the roughly decreasing (dashed lines) and increasing (solid lines) sets of means south across the Nearctic in *B. improba*; including Coloradan *B. acrocneuma* strongly reverses these clinal trends in each set at the Alberta–Colorado range disjunction.

(see Wilson & Brown, 1953). In certain aspects of coloration and maculation, *B. improba* from British Columbia appear superficially the closest to *B. acrocneuma* in the material we have analyzed. Yet on most metric characters quantified in the text North American arctic *B. improba* are closer than are Canadian subarctic *B. improba*, with Scandinavian arctic material occupying varied positions with respect to the others (see Fig. 32). Interestingly, Scandinavian arctic *B. improba* are the most similar to *B. acrocneuma* in several ventral wing-pattern characters, but, like North American arctic *B. improba*, present a general wing-pattern phenotype more divergent than Canadian subarctic *B. improba*. Local and within population variation strongly encroach upon broader geographic variation in *B. improba*, and character discordance seems to be common. The suitability of the *B. improba* trinomens as presently defined, especially in the Nearctic, therefore appears somewhat in doubt. Other multivariate work on intraspecific variation in *B. improba* generally supports this suggestion.

Little has been published on the ecology and habits of Nearctic *B. improba*, although the life history of Scandinavian arctic *B. improba* is partially known. In northwestern Finland, the presumed host (based principally on adult association) is *Salix herbacea* (L.), and



FIG. 33. Habitat of *Boloria acrocneuma* on Mt. Uncompahgre, Hinsdale Co., Colorado. The view is to the SE, at elev. approx. 4100 m. Adults fly across the slopes in the immediate foreground, and to the left of the path. Oviposition activity by females on and near the Snow Willow *Salix nivalis* was most frequently observed at lower left center, in front of the lighter colored slope. Photograph by Clifford D. Ferris.

populations occur in very rocky areas with late snow melt (Bruun & von Schantz, 1948). At present only several days' observations are available for *B. acrocneuma*. More detailed population studies on both species continue and will be reported elsewhere (Gall, Sperling, & Shaw, unpublished).

The colony site (Fig. 33) for *B. acrocneuma* is located several hundred meters SE of the summit of Mt. Uncompahgre, elev. approx. 4080–4140 m. The path to the peak (4361 m) bisects the type locality. This area is an exposed, northeast-facing high alpine meadow. It is covered with small rocks and merges with a scree slope to the north. Both males and females were flying in modest abundance (we estimated several hundred individuals *in toto*) as early as 0800 h on 30 July 1978 under calm, sunny, but brisk conditions. A pair was taken *in copula* at 0957 h resting in the vegetation on a steep rocky slope overlooking the main site. The wing-wear condition of the adults (intermediate and worn males, fairly fresh females) suggested that the flight season was at or just beyond the median date. Mark-release-recapture data from late July and early August 1979 indicate that daily adult numbers are on the order of 150 to 180 at peak flight. Adult activity is also exceedingly localized in space, in part to an area

where the preferred oviposition substrate and larval host-plant Snow Willow (*Salix nivalis* Hook.) occurs.

*Parnassius phoebus* (Fabr.), *Colias meadii* Edw., *Plebejus shasta* (Edw.), *Euphydryas anicia* (Dbldy.), *Oeneis taygete* Geyer, *O. melissa* (Fabr.), *Erebia callias* Edw., and *Pyrgus centaureae* (Rambur) fly at or near the colony site. *Colias scudderi* Reakirt, *C. eurytheme* Boisd., *Lycaena cupreus* (Edw.), *Agriades glandon* (Prunner), *Boloria titania* (Esper), *B. freija* (Thunberg), *Speyeria mormonia* (Boisd.), and *Erebia theano demmia* Warren (on even numbered years) fly in more sheltered areas above timberline at elevations from 3650–3850 m.

The southernmost limit presently known for *B. improba* in the Nearctic is Prospect Mountain, 8.3 km W of Mountain Park, Alberta, elev. 2740 m. This locality itself is a modest disjunction in the Canadian subarctic range of *B. improba*, and is over 1800 km from Mt. Uncompahgre. We consider that the observed allopatry between *B. acrocneuma* and *B. improba* reflects a post-Wisconsin glaciation loss of intermediate populations in a formerly more continuous distribution throughout the southern and central Rocky Mountains, and that these species have since been isolated. It seems highly unlikely that *B. acrocneuma* will prove widespread in distribution, since considerable collecting has been conducted in the major high altitude parts of Colorado other than the San Juan Mountains, and in high ranges of New Mexico and Utah. Such a distinctive butterfly would not have been overlooked if present. Although to date one colony is known, we feel careful searches will probably uncover additional colonies of *B. acrocneuma* in the San Juan Mountains.

We have carefully weighed the present and future conservational implications of disclosing precise locality data for the Mt. Uncompahgre population. We feel that extensive publicity of this unique, potentially fragile situation is the most positive option available for insuring a healthy future for this local endemic.<sup>3</sup> In the interim, pending further details on the biology and population dynamics of *B. acrocneuma*, we suggest collectors remove only very small series of adults from this population. Ecological and distributional data continue to be obtained so that knowledgeable statement concerning the

---

<sup>3</sup> A letter from the senior author to the U.S. Fish & Wildlife Service was accepted in December 1979 as a petition for status assessment within the context of Section 4 (c) (2) of the U.S. Endangered Species Act of 1973, as amended. A notice of review has been published (Federal Register 45:8029) to determine whether Endangered or Threatened status is warranted. Persons interested in this situation and those with pertinent additional information are urged to contact the senior author immediately at the Department of Biology, Yale University, New Haven, CT 06520; or the President of the Xerces Society, Larry Orsak, at the Department of Entomology, 201 Wellman Hall, University of California, Berkeley, CA 94720.

**Note added in proof:** Mark-release-recapture data from late July and early August 1980 indicate that daily adult numbers may be of the order of up to 250 at peak flight (compared to high estimate of 180 made in 1979).

conservational status of this species can be made. The possibility of a comprehensive management plan for the diverse and scenic Mt. Uncompahgre area is also presently being considered.

#### ACKNOWLEDGMENTS

We thank Charles L. Remington, James E. Rodman, Nancy A. Knowlton, Clifford D. Ferris, Kenelm W. Philip, Edward M. Pike, and Dale F. Schweitzer for editorial and taxonomic advice. C. D. Ferris also kindly provided the habitat photograph, and field assistance during 1979. James A. Scott and two anonymous referees offered appreciated criticism of the manuscript in its earlier stages. Thanks are also extended to Gerald J. Hilchie, E. M. Pike, and the American Museum of Natural History for providing specimens of *B. i. youngi* and *B. i. improbula*. The Biology Department of Yale University generously supplied computer time and partial travel expenses during 1979 to LFG, and John P. Dawson's technical expertise proved indispensable while trouble-shooting the phenetics program. A base for research during 1978 and 1979 was provided by the Rocky Mountain Biological Laboratory, Crested Butte, Colorado 81224.

#### LITERATURE CITED

- AYALA, F. J. 1975. Genetic differentiation during the speciation process. *Evol. Biol.* 8: 1-78.
- BROTHERS, D. J. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *Univ. Kansas Sci. Bull.* 50: 483-648.
- BRUUN, H. & M. VON SCHANTZ. 1948. Till kändedom om *Brenthis improba* Btl. ssp. *improbula* Bryk. (Lepid.). *Not. Ent.* 29: 82-89.
- BURNS, J. M. 1960. A new species of oak-eating *Erynnis* (Lepidoptera: Hesperidae) restricted to the southern cordillera of the United States. *Wasm. J. Biol.* 18: 147-160.
- CARDÉ, R. T., SHAPIRO, A. M. & H. K. CLENCH. 1970. Sibling species in the *Eurydice* group of *Lethe* (Lepidoptera: Satyridae). *Psyche* 77: 70-103.
- CLENCH, H. K. 1972. *Celastrina ebenina*, a new species of Lycaenidae (Lepidoptera) from the eastern United States. *Ann. Carnegie Mus.* 44: 33-44.
- DICE, L. R. 1943. *The Biotic Provinces of North America*. Univ. Mich. Press, Ann Arbor. 78 p.
- DOS PASSOS, C. F. 1964. A synonymic list of the nearctic Rhopalocera. *Mem. Lepid. Soc.* 1: 1-145.
- & L. P. GREY. 1945. A genitalic survey of Argynninae (Lepidoptera: Nymphalidae). *Amer. Mus. Novitates* 1296: 1-29.
- EHRlich, P. R. & H. K. CLENCH. 1960. A new subgenus and species of *Callophrys* (s.l.) from the southwestern United States (Lepidoptera: Lycaenidae). *Entomol. News* 71: 137-141.
- & A. H. EHRlich. 1967. The phenetic relationships of the butterflies. I. Adult taxonomy and the nonspecificity hypothesis. *Syst. Zool.* 16: 301-317.
- FREEMAN, T. N. 1956. The distribution of arctic and subarctic butterflies. *Proc. Tenth Int. Congr. Ent.* 1: 659-672.
- GALL, L. F. 1976. The status of *Satyrrium boreale* (Lycaenidae). *J. Lepid. Soc.* 30: 214-218.
- HARMAN, H. H. 1976. *Modern Factor Analysis*. Univ. Chicago Press, Chicago. 487 p.

- HENNIG, W. 1966. Phylogenetic Systematics. Univ. Ill. Press, Urbana. 263 p.
- HIGGINS, L. G. & N. D. RILEY. 1970. A Field Guide to the Butterflies of Britain and Europe. Collins, London. 380 p.
- KLOTS, A. B. 1951. A Field Guide to the Butterflies of North America, east of the Great Plains. Houghton Mifflin, Boston. 349 p.
- 1956. Lepidoptera, pp. 97–111. In S. L. Tuxen [ed.], Taxonomists' Glossary of Genitalia in Insects. Munksgaard, Copenhagen.
- KRUCKEBERG, A. R. 1957. Variation in fertility of hybrids between isolated populations of the serpentine species, *Streptanthus glandulosus* Hook. Evolution 11: 185–211.
- LAFONTAINE, J. D. 1970. A redescription of *Strymon borealis* Lafontaine (Lycaenidae). J. Lepid. Soc. 24: 83–86.
- MAYR, E. 1963. Animal Species and Evolution. Belknap, Harvard Univ. Press, Cambridge. 797 p.
- 1974. Cladistic analysis or cladistic classification? Zeit. fur Zool. Syst. und Evol. 12: 94–128.
- MICHENER, C. D. 1970. Diverse approaches to systematics. Evol. Biol. 4: 1–38.
- MOORE, J. A. 1967. Diploid and haploid hybridization of different populations of the *Rana pipiens* complex. J. Exp. Zool. 165: 1–20, 461–474.
- OLIVER, C. G. 1972. Genetic and phenotypic differentiation and geographic distance in four species of Lepidoptera. Evolution 26: 221–241.
- 1977. Genetic incompatibility between populations of the nymphalid butterfly *Boloria selene* from England and the United States. Heredity 39: 279–285.
- PARKS, J. M. 1968. Classification of mixed-mode data by R-mode factor analysis and Q-mode cluster analysis on distance function, pp. 187–192. Proc. Colloquium in Numerical Taxonomy, Univ. of St. Andrews.
- 1970. FORTRAN IV program for Q-mode cluster analysis on distance function with printed dendrogram. Kansas Geol. Survey Computer Contrib. 46: 1–32.
- PERKINS, E. M. & W. C. MEYER. 1973. Revision of the *Boloria epithore* complex, with description of two new subspecies (Nymphalidae). Bull. Allyn Mus. 11: 1–23.
- PIKE, E. M. 1978. Origin of tundra butterflies in Alberta. MS Thesis, Univ. of Alberta, Edmonton. 137 p.
- REMINGTON, C. L. 1968. A new sibling *Papilio* from the Rocky Mountains, with genetic and biological notes (Insecta, Lepidoptera). Postilla 119: 1–40.
- ROHLF, F. J. 1968. Stereograms in numerical taxonomy. Syst. Zool. 17: 246–255.
- & R. R. SOKAL. 1969. Statistical Tables. Freeman, San Francisco. 253 p.
- SNEATH, P. H. A., & R. R. SOKAL. 1973. Numerical Taxonomy: the principles and practice of numerical classification. Freeman, San Francisco. 573 p.
- SOKAL, R. R. 1975. Mayr on cladism—and his critics. Syst. Zool. 24: 257–262.
- & F. J. ROHLF. 1969. Biometry. Freeman, San Francisco. 776 p.
- STALLINGS, D. B. & J. R. TURNER. 1954. Notes on *Megathymus neumogeni*, with description of a new species (Megathymidae). Lepid. News. 8: 77–87.
- WARREN, B. C. S. 1944. Review of the classification of the Argynnidi: with a systematic revision of the genus *Boloria*. Trans. Roy. Entomol. Soc. London 94: 1–101.
- WHITE, M. J. D. 1978. Modes of Speciation. Freeman, San Francisco. 455 p.
- WILSON, E. O. & W. L. BROWN, JR. 1953. The subspecies concept and its taxonomic application. Syst. Zool. 2: 97–111.

APPENDIX  
Characters employed in phenetic analyses<sup>1</sup>

Character description <sup>2</sup>	Num- ber of states <sup>3</sup>	Char- acter weight- ing <sup>4</sup>	Character description <sup>2</sup>	Num- ber of states <sup>3</sup>	Char- acter weight- ing <sup>4</sup>
MALE GENITALIC CHARACTERS					
1. Length of aedeagus	C	1	35. Intensity of maculation distad from FW subbasal area	4	1
2. Length: width ratio of aedeagus	C	1	36. Extent of whitish suffusion on FW	3	2
3. Shape of caecum	2	3	37. Proportion of submarginal spots in cells	3	3
4. Basal width of ductus ejaculatorius	C	1	38. Width 5th: width 2nd FW postmarginal spots	C	1
5. Shape of rostellum	3	2	39. Relative size progression of postmarginal spots	3	2
6. Length of digitus	C	3	40. Length from margin to postmarginal spot in cell R <sub>4</sub>	C	1
7. Width of digitus at distal end	C	1	41. Length from margin to postmarginal spot in cell M <sub>2</sub>	C	1
8. Width of digitus at center	C	2	42. Shape of FW basal spot	3	3
9. Length digitus: length valve	C	3	43. Width postmedian band in cell M <sub>3</sub>	C	1
10. Shape of digitus spines	4	3	44. Distance from subapical spot to terminal postmarginal spot in cell R <sub>2</sub>	C	2
11. Number of digitus spines	3	1	45. Confluence of FW bands distad from subbasal area	3	3
12. Length of uncus	C	3	46. Number open centered spots along costal margin	4	3
13. Length: width ratio of uncus	C	1	47. Disjunction of FW postmedial band in lower limbal area	5	1
14. Length uncus: length valve	C	1	48. Angle of 3rd FW costal spot	3	3
15. Degree of uncus curvature	2	2	49. Antenna length	C	2
16. Shape of caudal section of tegumen	3	3	50. Length of antennal club	C	1
17. Width of tegumen at center	C	1	51. Length: width of antennal club	C	1
18. Degree of tegumen curvature	2	2	52. Length: width of FW	C	3
19. Length of dorsal arm of cucullus	C	1	VENTRAL WING-PATTERN CHARACTERS		
20. Shape of distal section of cucullus	3	2	53. FW ground color <sup>5</sup>	4	2
21. Terminal prong shape on cucullus	3	2	54. Degree of contrast in FW maculation <sup>5</sup>	3	2
22. Number of teeth on dorsal arm of cucullus	4	2	55. Separation of FW postmedial spots in upper limbal area <sup>5</sup>	3	1
23. Length of valve	C	3	56. Maculation contrast in HW discal area	4	3
24. Angle formed by harpe and costal arm	3	2	57. Extent of purplish cast on HW	3	3
25. Width of saccus	C	3	58. Form of postmedian-median HW row	4	3
26. Width of saccus: valve length	C	1	59. Extent of white-silver on postmedian-median HW row	5	2
27. Shape of distal part of saccus	3	2	60. Shape HW white costal spot	2	3
28. Width of costal arm	C	2	61. Coloration at FW apex <sup>5</sup>	2	1
29. Costal arm width: digitus length	C	2	62. Contrast FW veins with ground color	3	2
30. Costal arm width: valve length	C	3	DORSAL WING-PATTERN CHARACTERS		
DORSAL WING-PATTERN CHARACTERS					
31. Forewing ground color	4	2			
32. Degree of contrast in FW maculation	3	3			
33. Extent of HW melanization	4	2			
34. Extent of HW submedial spot	3	2			

APPENDIX  
Continued

Character description <sup>2</sup>	Number of states <sup>3</sup>	Character weighting <sup>4</sup>	Character description <sup>2</sup>	Number of states <sup>3</sup>	Character weighting <sup>4</sup>
63. Shape of wing margins	3	2	71. Length of postmedian-median row discal spot: FW length	C	2
64. Forewing length	C	2	72. Amount of darker coloration marginad of FW marginal spots	3	3
65. Relative width of FW maculation along costa	3	2	73. Amount of darker coloration distad of FW marginal spots	3	1
66. Form of HW margin spots & fringe <sup>5</sup>	3	2	74. Ground color shift above M <sub>2</sub> near submarginal spots	3	1
67. Color of FW veins <sup>5</sup>	3	2	75. Color of palpi on under-surface	4	2
68. Form of white spot basad of HW costal spot	4	1			
69. Offset of postmedian-median row below discal cell	3	1			
70. Length of postmedian-median row discal spot	C	1			

<sup>1</sup> The set of wing-pattern characters is a composite of those compiled in 1978 by us and others compiled more recently by students in an undergraduate evolutionary biology laboratory at Yale University. An array of male *Boloria* was given to them as an exercise in phenetic taxonomy (with no further instructions); their data returned a phenogram and ordination plot comparable to earlier versions obtained with our data. Of their 44 characters, 18 proved to be identical to ones we had used earlier; these were discarded, and the remaining 26 appended to our original list.

Characters were scored on the right side of genitalia (ventral view) and right wings, whenever possible. Fifty-nine missing values (e.g., no antennae) were encountered, representing 1.4% (59 of 4275) of the cells in the data matrices. These cells were filled with the means from larger samples for that population or immediate geographic region.

We also caution here against a potential complication inherent in mixing ratios and size-scaled variables with raw dimensions in multivariate analyses. Ratios and size-scaled variables sometimes exhibit non-linear relationships which may distort linear matrix analyses, such as principal components (see, for example, the journal *Systematic Zoology* [vol. 27, pp. 61-83; 1978] for diverse opinions on this subject). Since discussing the effects of such mixing is beyond the scope of this paper, we simply note that phenograms based on the sets of characters excluding ratios and size-scaled variables returned identical taxonomic decisions.

<sup>2</sup> Terminology follows dos Passos & Grey (1945) and Klots (1956).

<sup>3</sup> A "C" indicates a continuous variable; full character state descriptions are available from the senior author upon request.

<sup>4</sup> Number indicates principal component in ordination plot on which this character is most heavily weighted (these are ranked factor loadings of the original characters; see Fig. 31).

<sup>5</sup> Indicates characters not scored in females.