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## A GENITALIC SURVEY OF ARGYNNINAE (LEPIDOPTERA, NYMPHALIDAE)

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While preparing manuscript for a revision of the North American butterflies usually referred to the genus *Argynnis* Fabricius (1807, p. ix), it seemed advisable to publish separately our notes on the genitalia of some of the associated world species. Our intention is to give a skeleton outline of genitalic data for the subfamily, sufficiently complete to demonstrate the peculiarities of the Nearctic species and to serve as a basis for comparisons.

When the present paper was submitted for publication, the monograph by Warren<sup>1</sup> reviewing the classification of Argynnidi, which includes a revision of *Boloria* Moore (1900, p. 243), to which consideration is given in the discussion toward the end of this paper, had not been published. Warren points out, as we do, the excellent usefulness of the male genitalia in giving better classificational results than those hitherto obtained by the use of wing pattern, especially in providing unfailing generic characters. We are keeping to the older classification except in those instances where the need of recognizing outstanding genitalic groups is imperative, and we are proposing no new names since Warren's monograph is complete for those groups which he has studied so painstakingly. Although some duplication is unavoidable because of our intention to give fairly complete subfamily data, our paper is written primarily for American students and is published in the belief that to some little extent it may supplement Warren's revision and perhaps further serve to call attention to the results obtainable by genitalic analysis. Our purpose is to establish the isolated

position of the Nearctic species, and to do this it proves necessary to discuss Argynninae of the world, since the popular generic conceptions are inadequate or erroneous.

The systematic arrangement follows obvious genitalic analogies which give basis for a rough preliminary separation of related species, following tangible similarities. The exact sequence is merely tabulative; other data would have to be considered before attempting further refinement to show phylogeny.

The dissections, genitalic slides, and drawings are the work of the junior author, and unless otherwise indicated the specimens and slides are in his possession. The figures should be used with caution, if at all, for specific identifications; the dissections were not done in revisional amplitude and are intended only to establish relationships and subfamily range of variation in the sexual structures.

The terminology used for the various parts of the male genital armature is indicated by figure 54 which shows the complete genitalia of *Speyeria atlantis* (Edwards) (1862a, p. 54) and is further defined below.

### DESCRIPTION OF THE MALE GENITAL ARMATURE

Figure 54

The large hood-shaped *tegumen* (ninth segment) is a modified tergite to which the attached *vinculum* is the accompanying sternite of the so-called genitalic ring. The *vinculum* is usually enlarged ventrally, forming a *saccus*, which is well developed in Argynninae but never greatly extended. Interesting features found in many species of this subfamily are the paired, flattened

<sup>1</sup> Warren, B. C. S., Review of the classification of the Argynnidi: with a systematic revision of the genus *Boloria*, 1944, Trans. Roy. Ent. Soc. London, vol. 94, pp. 1-101, pls. 1-46, figs. 1-317.

lobes attached within and near the base of the tegumen which are best seen cephalad but may be extruded for lateral study. These do not seem to be identical with any of the named accessory organs. If they are representative of a gnathos they are indeed aberrant. Judging from the articulation they may be homologous with the transtilla of certain other Lepidoptera, but it seems safest to apply a separate designation. We are terming them *vanni* (singular, *vannus*; Latin, a fan). The tegumen is often broken into more or less separately sclerotized areas, of which a small, outermost ventro-caudal segment is usually partly free or joined only by membrane, yet with very remote analogy to a subscaphium or to a peniculus. There is a dorsal area in the tegumen which is membranous. The *anellus* is immediately above and caudad of the saccus. In figure 54 a separate view, cephalad, is given since the anellus lies within the armature at a right angle to the lateral plane. In form, it is a pair of extended lobes, providing support for the *aedeagus*. The latter is conspicuous, often with distinct modifications in shape, sclerotizations, and cornute armature.

The *valves*, paired, flattened organs said to be derived from the pedal appendages of the ninth segment, are articulated dorsally at the juncture of the vinculum and the tegumen and ventrally upon the saccular portion of the vinculum and to the anellus. Since these valves vary greatly in form, there is a special terminology for the parts. Three general areas are recognized. We have used the term *dorsal lobe* for the free basal portion of the costa; this bears the hook-like sclerotization by which dorsal articulation is made to the genitalic ring. The costal area narrows medially to little more than a sclerotized margin where it joins with the *cucullus* or central division of the valve. The "superior process" (or processes) is usually considered to belong with the costa. In Nearctic *Speyeria* Scudder (1872, p. 23) a heavily sclerotized plate replacing the dorsal distal extension has been separately termed a *digitus*. These dorsal specializations are somewhat to the rear of, and often partly concealed by, the variously modified distal portions of the

*cucullus*. In *Boloria* the "inferior process" of the valve, which we call a *cucullus termen* (not realistically portrayed on a plane surface, being three-dimensional like the sharply curved prow of a boat), is formed, as figures 1-21 suggest, by the terminal valve sclerotization. In dissections that have had no pressure this *cucullus termen* usually lies at almost a right angle to the valve surface, and in making slides to display in so far as possible all of the features that appear to be of special interest, we have arranged the separately dissected valve so that the *cucullus termen* is uniformly bent dorsad to show its outline. Many species of *Argynnis* have an oblique, spiny ridge or *crista obliqua* extending from the median area of the *cucullus* and joining to the costa. This "crista obliqua" of Petersen (1904, p. 50, fig. 18) may be homologous with the harpé as the latter term is used by McDunnough (1911, p. 188) judging from Forbes' (1939, pp. 7, 9) analysis of the musculature, or possibly the harpé also includes the distal dorsal process. The heavy sclerotization often found immediately basad or distad of this spiny ridge on the upper border of the *cucullus* appears to be a clasping specialization. The bell-shaped dark area often noticed near the base of the valve is formed partly by the roll of the *sacculus* (ventral and foremost portion of the valve) at that point but is due in part to interior processes leading to the anellus. The *uncus* is considered as representing the tergite of the tenth segment. The corresponding sternite (subscaphium and/or socius) often is atrophied or absent in Argynninae. The *uncus* often is specifically varied in shape as well as being of important diagnostic value in grouping related species. It is prominently located, attached to the dorsocaudal portion of the tegumen. Definite characters may occur in any of the parts of the whole armature.

Further remarks concerning the genitalic peculiarities will be found under the appropriate generic and specific headings. Figures 1-48 give selected views of the anellus, aedeagus, valves, and uncus of the species studied.

### DESCRIPTION OF THE FEMALE GENITAL ARMATURE

No survey of the female genital armature in Argynnninae has been attempted by us. We have investigated that of the Nearctic genus *Speyeria*, finding some helpful differences (figs. 52, 53). It seems likely that the other groups would yield similarly valuable hints as to phylogeny and further aids toward specific determinations; therefore we give an abbreviated description of the morphology.

The external anatomy, including thoracic articulation, spiraculation, and details beyond the seventh (last regular) segment, may be studied prior to dissection. The ovipositor lobes of the tenth segment are well extruded, but the *apophyses* or ovipositor struts are partly concealed by the telescoped collar of the ninth segment and by the eighth segment which forms the so-called genital plate. The *ostium*, notch of the vaginal opening, is at the base of the eighth sternite, and there is a membranous protrusion between the seventh and eighth tergites, which we call the *dorsal gland*. We are uncertain whether this is a scent pouch or the cement-forming *colleterial gland* (Torre-Bueno, 1937, pl. 3, fig. 2). Many of the interior organs having to do with insemination and ovulation are so complex and so delicate that morphological comparisons are very difficult. Dissections should be preceded by a staining process and by a glycerin to water transfer so that these membranous parts may be properly dilated and made easily visible. The well-sclerotized *ductus bursae* leads directly from the ostium to the *bursa copulatrix*, which sometimes has an attached sac or *secondary bursa*; these parts are relatively easy to study. There is no *signum* (sclerotized or corneous area) on the bursa of *Speyeria*.

### Argynnninae

The genera *Boloria* Moore, *Brenthis* Hübner ([1819], Verzeichniss bekannter Schmettlinge [sic], 2d signature, p. 30), *Argynnis* Fabricius, *Speyeria* Scudder, and *Euptoieta* Doubleday (1848, p. 168) are similar genitally and placed by us in Argynnninae. In these genera, within a diversity of genitalic forms, there are basic

resemblances which can be appreciated best after comparisons are made with genera which usually are listed near the argynids. (For example, *Melitaea*, *Phyciodes*, and *Chlosyne* are entirely different in genitalic structure.) *Euptoieta* is aberrant but is retained here because of customary usage and on account of a slight relationship suggested by wing pattern and genitalic similarity. In some respects *Euptoieta* is intermediate to *Heliconiinae* (Michener, 1942, figs. 9-17) which is the only group of butterflies in which we have perceived any vague genitalic resemblances to Argynnninae. Except for some imperfect linkage to the heliconians, the argynids are distinct from other nymphalids and would appear to merit recognition as a subfamily. Forbes has suggested (*in litt.*) that we investigate *Basilarchia* and certain African genera to see what relationship they might have to Argynnninae, a project which we have been unable to add to the work already undertaken. It is interesting to note that Grote (1900, p. 7) defined by wing venations approximately the major groupings which are indicated by the genital armature, further substantiating the naturalness of the associations.

### BOLORIA MOORE

*Boloria* MOORE, 1900, p. 243. GENOTYPE: *Papilio pales* [Denis and Schiffermüller], 1775, p. 177. FIXATION: Original designation monotypic.

*Clossiana* REUSS, "1921" [1922], p. 225. GENOTYPE: *Papilio selene* [Denis and Schiffermüller], 1775, p. 321. FIXATION: By original designation.

Under this genus we place the Holarctic species that commonly have been known as *Brenthis*, making no attempt to give more than a brief summary of outstanding peculiarities noted in the male genital armature. As listed here, no subdivisions are made and no emphasis is placed upon definition of species and subspecies or upon order of arrangement. The outstanding distinctions whereby these species are unfailingly separable from the so-called argynids are of interest because of confusing statements in the literature. Although some refinements in classification could be made, the series of insects listed below are

roughly homogeneous in having the valves relatively simple as to the amount of sclerotized development, an aedeagus which is basally closed and an uncus which is bifid (fig. 51), characters which distinguish *Boloria* from other major groups in the subfamily.

### ***Boloria thore* (Hübner)**

#### Figure 1

HÜBNER, [July, 1803-1804], Sammlung europäischer Schmetterlinge, [vol. 1], pl. 111, figs. 571-573.

SPECIMEN FIGURED: Europe, ex J. Doll collection, ex the Museum of Comparative Zoölogy, genitalic slide no. 309.

*Boloria* may be divided into two groups, depending upon the shape, size, and amount of sclerotization of the dorsal-distal lobular portion of the aedeagus. The *thore* group (figs. 1-15) comprises the majority of the species. In *thore*, the lobes on the aedeagus are small, and the organ also is comparatively small. The dorsal arm and the cucullus termen both are smooth or only very slightly spinose.

### ***Boloria improba* (Butler)**

#### Figure 2

BUTLER, 1877, p. 206.

SPECIMEN FIGURED: Torne Trask, Lapland, 3500 feet, July 9, 1937 (Higgins), genitalic slide no. 305, in the American Museum of Natural History.

It is likely that *improba* deserves specific rank. The few dissections which we have made are hardly decisive but point to the conclusion that *improba* is wrongly placed with *frigga* by McDunnough (1938, p. 16) and indicate a separation from *thore*.

### ***Boloria frigga* (Thunberg)**

#### Figure 3

THUNBERG, 1791, p. 33.

SPECIMEN FIGURED: Riding Mountains, Manitoba (J. May), genitalic slide no. 346.

The dorsal arm and the cucullus termen are very much more spinose than in *improba* and *thore*. It is believed that *frigga* has a very wide range and subspeciation, expressed in North America by *saga* (Staudinger) (1861, p. 350), *kriemhild* (Strecker) ([1879], p. 1854, pl. 1, figs. 5, 6) *sagata* (Barnes and Benjamin) (1923, p. 146), *epithore* (Edwards) (1864, p. 504),

*gibsoni* (Barnes and Benjamin) (1926, p. 92), and other varying populations. Specific separations, if any can be made, become a task for revisional study.

### ***Boloria toddi* (Holland)**

#### Figure 4

HOLLAND, 1928, p. 45.

SPECIMEN FIGURED: Salem, Virginia, July 14, 1940 (C. Gottschalk), genitalic slide no. 345.

Since *bellona* (Fabricius) (1775, p. 517, no. 317) is unavailable as a homonym, Holland's name for a northern Quebec population has priority over *ammiralis* (Hemming) (1933b, p. 276), which was proposed to replace *bellona*, a southern subspecies. Genitally, while still in a group of very similar species, this insect appears to be separable as one of the very few entities confined to the Nearctic fauna. The association with *frigga* is evidenced by the spiny cucullus termen, although the dorsal arm is only very slightly spined. The sclerotized developments in the distal portions of the aedeagus are somewhat atrophied. Purely as a speculation, one might wonder if *toddii* is not a comparatively ancient species. These sclerotizations are almost undoubtedly the homologues and probably the forerunner of the extensively cornute and specialized development of the aedeagus found in the argynnids.

### ***Boloria selene* ([Denis and Schiffermüller])**

#### Figures 5, 51

[DENIS AND SCHIFFERMÜLLER], 1775, p. 321.

SPECIMEN FIGURED: Hamburg, Germany, May 30, genitalic slide no. 354.

The Nearctic *myrina* (Cramer) ([1777], vol. 2, p. 141, pl. 189, figs. B, C) and its associated variation are genitally, as well as in appearance, like *selene* and no doubt belong with it. The interior sclerotized development basad of the membranous distal lobes of the aedeagus is small; from it there are fairly well-defined light sclerotizations along the lobes. The dorsal arm bears several small terminal spiculations. The cucullus termen is not spinose and appears to be constantly recognizable in outline.

**Boloria polaris** (Boisduval)

## Figure 6

BOISDUVAL, "1829" [1828], p. 15.

SPECIMEN FIGURED: Rama, Labrador, 1894 (A. Stecker), genitalic slide no. 264, in the Museum of Comparative Zoölogy.

The internal sclerotization basad of the aedeagal lobes is spiny-serrate with lightly sclerotized processes upon the lobes. These variations, within loosely arranged and rather amorphous membranous or very delicately sclerotized tissues, are not easy to describe or to draw accurately. Within certain limits the repetitive similarities observed in the dissections of related species suggest that despite individual differences, ease of distortion, and difficulty of exact comparisons, the aedeagus has characters of value. Certainly in *polaris* it is indicative.

**Boloria jerdoni** (Lang)

## Figure 7

LANG, 1868, p. 34.

SPECIMEN FIGURED: (No data), *ex* Weeks collection, no. 178, genitalic slide no. 316, in the Museum of Comparative Zoölogy.

This Asiatic species displays a valve modification in a process extending from the dorsal basal lobe, although the other differences from the norm of the present group are not striking. The dorsal arm is short and bears long, delicate, hair-like spines in addition to the usual setae. The cucullus termen is smooth.

**Boloria gong** (Oberthür)

## Figure 8

OBERTHÜR, 1884, p. 15, pl. 2, fig. 9.

SPECIMEN FIGURED: Loutsechiang, Yunnan Province, China (A. Genestier), genitalic slide no. 295, in the American Museum of Natural History.

Only passing mention need be accorded to this rare Himalayan species, differing in slight detail as shown by the figures but apparently not greatly modified in structure from preceding entities. It is to be noted that the sclerotizations in the distal trough of the aedeagus are rather large, with extended sclerotic processes which are comparatively more spiny-serrate than in related species. The dorsal arm is short, distally swollen with a spiny tip.

The cucullus termen is smooth, with an outline which seems to be characteristically distinct.

**Boloria haberhaueri** (Hemming)

## Figure 9

HEMMING, 1933b, p. 275 (= *Argynnis hegemone* Staudinger, 1881, p. 292).SPECIMEN FIGURED: Naryn, [Siberia], *ex* Weeks collection, no. 2854, genitalic slide no. 319, in the Museum of Comparative Zoölogy.

The superficial wing pattern suggests a relationship to *aphirape* (Hübner) ([December 24, 1799–April 13, 1800, vol. 1], pl. 5, figs. 23–25) but, as will be seen by comparison of the juxtaposed figures, the two species are very distinct. In *haberhaueri* the dorsal arm is short with long conspicuous spines; the cucullus termen is smooth, long, and slender, and the aedeagus is of the type usual in this group.

**Boloria aphirape** (Hübner)

## Figure 10

HÜBNER, [December 24, 1799–April 13, 1800], Sammlung europäischer Schmetterlinge, [vol. 1], pl. 5, figs. 23–25.

SPECIMEN FIGURED: Riding Mountains, Manitoba, July 12, 1938 (J. May), genitalic slide no. 254.

We believe that *aphirape* should be easy to identify in all of the numerous Holarctic populations by reason of the wide, bilobed dorsal arm. Also, the lack of the usual long sweeping cucullus termen is a peculiarity shared only by *pales* among the species here placed in *Boloria*. In other respects *aphirape* is genitally like associated species with only minor differences.

**Boloria alberta** (Edwards)

## Figure 11

EDWARDS, 1890, p. 113.

SPECIMEN FIGURED: Banff, Alberta, July 13, 1930 (J. May), genitalic slide no. 304, in the American Museum of Natural History.

The dorsal arm is well spined along the upper terminal margin, and the cucullus termen ends in two points. The long, dorsally upcurving tip of the aedeagal tube also appears to be specifically diagnostic. This insect is of limited habitat. Any suspected forms which would extend the known range of this species should be easy

to identify with *alberta* by reason of its genitalic peculiarities. Possibly *distincta* (Gibson) (1920, p. 25i) belongs here, but we have no specimen for dissection.

### ***Boloria astarte* (Doubleday)**

Figure 12

DOUBLEDAY, 1847, pl. 23, fig. 5.

SPECIMEN FIGURED: (*Amphilochus*), Transbaikal, Siberia, ex Weeks collection, genitalic slide no. 311, in the Museum of Comparative Zoölogy.

The North American *astarte* is so like the Siberian *amphilochus* (M. [sic] Ménétris) (1858, p. 213) that we had justifiable suspicions of finding, as we do, that they are genitally identical. The cucullus termen bears several large spines, and the dorsal arm is distally enlarged to an angular lobe. Another distinguishing feature is found in the area of setae which is located dorsad and caudad upon the tegumen. The latter development apparently is unique in the subfamily, other species having at most a very few delicate setae, seen only under high magnification.

### ***Boloria pales* ([Denis and Schiffermüller])**

Figure 13

[DENIS AND SCHIFFERMÜLLER], 1775, p. 177.

SPECIMEN FIGURED: Zermatt, Valais, Switzerland, July 19, 1934, genitalic slide no. 327.

This genotypical species is instantly separable by the somewhat aberrant male genital armature. The heavy spiculations upon the aedeagus differ only in degree from the condition observable in related species. By evidence of the valves, *pales* and *aphirape* are closely related, being the only species of *boloria* known to us that lack the extended cucullus processes. The dorsal arms are likewise analogous. Both *pales* and *aphirape* have the bifid uncus of *Boloria*, but in *aphirape* it is very slender, while in *pales* it is unusually stout.

### ***Boloria dia* (Linnaeus)**

Figure 14

LINNAEUS, 1767, p. 785, no. 207.

SPECIMEN FIGURED: France, ex Eddy collection, genitalic slide no. 236, in the Museum of Comparative Zoölogy.

In *dia* we note that the lobes of the anellus arise from a somewhat modified basal

plate. However, although the figures show rather pronounced differences in the shape of the anellus for various species, this is partly due to the condition of individual specimens. The differences are specific to some extent, but the anellus is very easily distorted as it is attached to the valves and varies in outline when they are manipulated. The aedeagus of *dia* is quite sufficient to provide reliable diagnosis.

### ***Boloria freija* (Thunberg)**

Figure 15

THUNBERG, 1791, p. 34, pl. 2, fig. 14.

SPECIMEN FIGURED: Nordegg, Alberta, May 2, 1933, genitalic slide no. 265.

This insect has an extensive Holarctic subspeciation. Genitally it is unique, although the characteristically sagittate outline of the aedeagus is due not so much to a basic difference as to an adaptation of form of the terminal lobes. The dorsal arm and cucullus termen are also distinct in outline. The figure obviates further comment. There is no reason to confuse any of the subspecies of *freija* with those of any other species.

### ***Boloria selenis* (Eversmann)**

Figure 16

EVERSMANN, 1837, p. 10.

SPECIMEN FIGURED: Kirin Province, Manchuria, June 3, genitalic slide no. 257.

The remaining species here included in *Boloria* (figs. 16-21) agree with *selenis* in peculiarities of the aedeagus. The distal lobes are extensively sclerotized, there is an increase in the size of these lobes, and the whole aedeagus becomes of formidable proportions in comparison to the remainder of the genital armature. Also, the process arising from the aedeagal trough becomes more sclerotized and notably spinose. The purely specific features will need close attention in work of a revisional nature, but a very helpful preliminary division of species is achieved by noticing that the type of aedeagus described above is readily distinct from that of preceding entities and is peculiar to those that follow. It is interesting to find fully developed structural divergencies in species so superficially alike as are *selene* (fig. 5) and *selenis*,

for example. The inference is that by means of genitalic comparisons aberrant specimens, strange appearing new subspecies, and undetermined specimens of *Boloria* can be related to the proper species or at least to a species group with less danger of error than is possible by reliance upon pattern of the wings.

In the specimens of *selenis* that were examined the dorsal arm is slender and spined only very lightly at the tip. The cucullus termen has several distinct spines and a thorn-like termination. The aedeagal lobes are heavily sclerotized on the edges but are relatively membranous centrally and basad. The spinose process basad of the lobes is short and rounded. A close study of related species, which have somewhat similar characters, would be required before it would be possible to say that certain features were invariable in *selenis*.

### ***Boloria euphrosyne* (Linnaeus)**

Figure 17

LINNAEUS, 1758, p. 481, no. 142.

SPECIMEN FIGURED: Hamburg, Germany, July 21, genitalic slide no. 355.

The dissections of *euphrosyne* reveal a dorsal arm which is somewhat swollen distally with only a very few small spines along the terminal outline. The cucullus termen is spinosely serrate. It is rather short, compressed, nearly square in outline, except for the short terminal spine, and apparently is constant in these respects. The aedeagus is similar to the type described under *selenis*.

### ***Boloria chariclea* (Schneider)**

Figure 18

SCHNEIDER, 1794, p. 588.

SPECIMEN FIGURED: McKinley Park, Alaska, July 29, 1930 (Fraser), genitalic slide no. 308, in the American Museum of Natural History.

One of the tasks in a revision of *Boloria* will be to unsnarl the subspeciation and the synonymy under *chariclea* and *rossicus* (Hemming) (1933b, p. 276). If *chariclea* is valid as a species, both it and *rossicus* are circumpolar in distribution with subspecies which we must recognize and define, yet both species are genitally very similar. The insect considered here is

not the "*chariclea*" of North American literature and of nearly all American collections but is a northern butterfly with which the majority of students are unfamiliar. Under the name we associate *arctica* (Zetterstedt) (1840, p. 899), *obscurata* (M'Lachlan) (1878, p. 110), and *bütleri* (Edwards) (1883, p. 32).

### ***Boloria rossicus* (Hemming)**

Figure 19

HEMMING, 1933b, p. 276 (= *Papilio amathusia* Esper, [1784], p. 170, pl. 88, figs. 1, 2).

SPECIMEN FIGURED: Manteux, Germany, June 24, genitalic slide no. 356.

Following the suggestions of Dr. A. B. Klots, we find that several well-known Nearctic insects are very similar to *rossicus*. The populations that have been named *montinus* (Scudder) (1863, p. 166), *boisduvalii* (Duponchel) (1832, p. 127, pl. 20, fig. 4), *grandis* (Barnes and McDunnough) (1916, p. 223), *helena* (Edwards) (1871, p. 268), *ingens* (Barnes and McDunnough) (1918, p. 71, pl. 11, figs. 5, 6), and *rainieri* (Barnes and McDunnough) (1913, p. 96, pl. 2, figs. 1-4) are genitally and superficially like this European insect. The variation in the male armature among these North American representatives may be greater, judging from the few dissections, than the differences observed between *rossicus* and *chariclea*. We are not in a position to make definite comment other than to note the close genitalic relationships. The cucullus termen is more sclerotized and less elongate, therefore more difficult to bend to secure a plane outline in a slide than is the case with most of the other species in *Boloria*, and the bending results in some distortion. The lobes of the anellus are large in size and possibly are diagnostic of the species in their shape.

### ***Boloria oscarus* (Eversmann)**

Figure 20

EVERSMANN, 1844, p. 588, pl. 14, figs. 1a, 1b.

SPECIMEN FIGURED: "Tunkinsk, Weisgbg., sudwesti Irkutsk," [Siberia], 2060 m [eters], July, ex Weeks collection, no. 421, genitalic slide no. 318, in the Museum of Comparative Zoölogy.

This Siberian butterfly belongs genitally with the *selenis* group but is specifically distinct. The cucullus bears a long, large

terminal spine with a smaller spine at the outer angle and is smooth except for these processes. On the valve there is a serration which by position is analogous to a rudimentary crista. This is observable under close examination in many of the species of *Boloria*. The saccus is unusually heavy and very noticeable because in the majority of the species of *Boloria* the saccus is only slightly wider than the remainder of the vinculum. The aedeagus is relatively large.

### *Boloria angarensis* (Erschoff)

Figure 21

ERSCHOFF, 1870, p. 112.

SPECIMEN FIGURED: "Transbaikal, mer. occ. Borochojewa, Maichan Montes," [Siberia], 800 m[eters], July, *ex* Weeks collection, no. 556, genitalic slide no. 317, in the Museum of Comparative Zoölogy.

A unique, large, heavily serrate cucullus termen insures the genitalic recognition of *angarensis*. The saccus is well developed as in *oscarus*. The uncus of *angarensis* and of the two species immediately preceding have been figured merely to indicate the similarities which prevail in this organ throughout *Boloria*.

### BRENTHIS HÜBNER

*Brenthis* HÜBNER, [1819], Verzeichniss bekannter Schmettlinge [sic], 2d signature, p. 30. GENOTYPE: *Papilio hecate* [Denis and Schiffermüller], 1775, p. 179. FIXATION: Scudder, 1872, p. 24.

It is apparent that *Brenthis* with genotype *hecate* cannot apply to the numerous species which have been called brentheids in the past. The *hecate* group consists of the three species listed below. They are confined to the Old World and are structurally distinct from the large Holarctic group heretofore listed under *Boloria*. They are likewise wholly distinct from all of the variously modified species of the *Argynnis* complex. *Brenthis* is in some respects intermediate between *Boloria* and *Argynnis*, as is further noted below.

### *Brenthis hecate* ([Denis and Schiffermüller])

Figure 22

[DENIS AND SCHIFFERMÜLLER], 1775, p. 179.

SPECIMEN FIGURED: Hungary, genitalic slide no. 79.

### *Brenthis ino* (Rottemburg)

Figure 23

ROTTEMBURG, 1775, p. 19.

SPECIMEN FIGURED: "Europa," *ex* J. Doll collection, genitalic slide no. 249, in the Museum of Comparative Zoölogy.

### *Brenthis daphne* ([Denis and Schiffermüller])

Figure 24

[DENIS AND SCHIFFERMÜLLER], 1775, p. 177.

SPECIMEN FIGURED: White Capped Mountains, Korea, July, 1933, genitalic slide no. 282.

We see that these Palearctic species are very similar genitally, and we have not attempted to find separating constancies. As in *Argynnis*, there is a long, spinose crista joining to a free dorsal arm. Centrad and basad on the valves we note all of the sclerotizations which appear in *Argynnis*. The aedeagal lobes are membranous, with the interior armature only delicately sclerotized, and the organ is completely open, basally, as in *Argynnis*. The uncus, however, is similar to the type found in *Boloria*, with divided tip but distinguished by having a third, short, central projection (seen dorsad or ventrad) by which *Brenthis* is separable as a distinct genus.

### ARGYNNIS FABRICIUS

*Argynnis* FABRICIUS, 1807, p. ix. GENOTYPE: *Papilio paphia* Linnaeus, 1758, p. 481, no. 138. FIXATION: Latreille, 1810, p. 440. VALIDATED: 1910, International Commission on Zoological Nomenclature, Opinion 11.

*Argyreus* SCOPOLI, 1777, p. 431. GENOTYPE: *Papilio niphe* Linnaeus, 1767, p. 785, no. 208 (= *Papilio hyperbius* Linnaeus, 1763, p. 408, no. 75). FIXATION: Reuss, 1928, p. 146.

*Issoria* HÜBNER, [1819], Verzeichniss bekannter Schmettlinge [sic], 2d signature, p. 31. GENOTYPE: *Papilio lathonia* Linnaeus, 1758, p. 481, no. 141. FIXATION: Scudder, 1875a, p. 198.

*Acidalia* HÜBNER, [1819], Verzeichniss bekannter Schmettlinge [sic], 2d signature, p. 31. GENOTYPE: *Papilio niphe* Linnaeus, 1767, p. 785, no. 208 (= *Papilio hyperbius* Linnaeus, 1763, p. 408, no. 75). FIXATION: Scudder, 1875a, p. 101.

*Argyronome* HÜBNER, [1819], Verzeichniss bekannter Schmettlinge [sic], 2d signature, p. 32. GENOTYPE: *Papilio laodice* Pallas, 1771, p. 470. FIXATION: Scudder, 1875a, p. 120.

*Argyrea* BILLBERG, 1820, p. 77. GENOTYPE: *Papilio paphia* Linnaeus, 1758, p. 481, no. 138. FIXATION: Hemming, 1933a, p. 197.



*Damora* NORDMANN, 1851, p. 439. GENO-TYPE: *Damora paulina* Nordmann, 1851, p. 440 (= *Argynnis sagana* Doubleday, 1847, pl. 21, fig. 1). FIXATION: Original designation monotypic.

In the species of this genus the uncus is never divided but is singly tipped. The valves are more or less complexly sclerotized; the aedeagus is wholly open, basally, and usually very cornute.

We see no possibility of arranging the argynnis into a progressive genitalic series. The related species are easily grouped, but many questions of phylogeny are left unanswered. Aside from the obviously related species there are several that are unique; by the nature of the problem an arrangement must be somewhat arbitrary even when other data are considered along with the genitalic evidence. The present sequence is not defended as being justified by graduated differences in the material; it is hard to see how a complete statement of the relationships could be demonstrated by the genital armature. We offer no definite classificatory proposals but will suggest some groupings in the notes that follow. A formal subdivision of the extreme genitalic heterogeneity into series of anything like comparable value would entail recognition of several small or monotypical genera or subgenera.

### *Argynnis cytheris* (Drury)

Figure 25

DRURY, 1773, vol. 2, p. 7, pl. 4, figs. 3, 4.

SPECIMEN FIGURED: Tofo, Chile, May 26, 1917 (T. Hallinan), genitalic slide no. 291, in the American Museum of Natural History.

It has been impossible to survey the Andean distribution of *Argynnis*. The specific names are based upon single specimens or upon short type series in European repositories. Judging from Lehmann (1913, pp. 426-429, pl. 87), there are only two or three South American entities, with extensive synonymies. Dissections from the short series of *cytheris* in the American Museum of Natural History were studied with much interest. The structural uniqueness which was found is probably no more than is to be expected when the isolation of the habitat is recalled. We are eager to learn if the other

Andean species are of similar genitalic type. The relationship, as far as definite placement is suggested, seems to be to the three species that follow. There is a temptation to speculate that these may be very ancient entities.

### *Argynnis hanningtoni* Elwes

Figure 26

ELWES, 1889, p. 558.

SPECIMEN FIGURED: Tumutumu, K[enya] C[olony], October 20, 1861, ex Loveridge collection, genitalic slide no. 310, in the Museum of Comparative Zoölogy.

African argynnis are virtually nonexistent in North American collections. Professor Nabokov has lent us specimens of *hanningtoni* from the short series in the Museum of Comparative Zoölogy, along with other substantially helpful loans which we gratefully acknowledge. Professor Carpenter of Oxford University has donated African material for which we are also thankful. Judging from this small accumulation, the African variation is closely related to *gemmata* Butler (1881, p. 32). The insect known as *excelsior* Butler (1895b, p. 729, pl. 44, fig. 4) apparently is a *hanningtoni* subspecies. A dissection of *smaragdifer* Butler (1895a, p. 629, pl. 35, figs. 1, 2) reveals that it is a species distinct from *hanningtoni*, with less prominent aedeagal lobes. It is very similar to *gemmata* in wing pattern and genitalic features.

### *Argynnis lathonia* (Linnaeus)

Figure 27

LINNAEUS, 1758, p. 481, n. 141.

SPECIMEN FIGURED: Darmstadt, Germany (H. Noack), genitalic slide no. 349.

This is the genotype of *Issoria*. The name can be used for the African species and for *gemmata* as well. Although the valve armature of *lathonia* is somewhat more developed, the sclerotizations are found merely in greater degree and not so changed in type as might at first appear. The two spines on the valve terminalia are indicative of *lathonia*. In *Issoria* there is a partly membranous complexity below the uncus which is only suggested in the figures. (Kusnezov [1915, vol. 1, p. cxx] shows this structure in greater detail and

calls it a subscaphium. We doubt the applicability of his term.) The spur-like protrusions from the tegumen-vinculum juncture, called the apices angulares by Kusnezov (*loc. cit.*), apparently are a part of the tegumen.

### *Argynnis gemmata* Butler

Figure 28

BUTLER, 1881, p. 32.

SPECIMEN FIGURED: Tibet, genitalic slide no. 276.

Specimens of *altissima* Elwes (1882, p. 403, pl. 25, fig. 8) and of *eugenia* Eversmann (1847, pt. 2, p. 68) have been found to be in close agreement with *gemma* which would extend the range of this species or species group to include much of Central Asia. One cannot fail to marvel at the distribution presented by the *Issoria* group. Fascinating guesses regarding ancestral *Argynnis* stocks are not intended to be a part of this survey, but the insects of this group, in wing pattern, venation, structure, and distribution, comprise the extreme fringe of the genus to which they belong. They have been placed by past authors wherever thought to be least conflicting but here are seen to be rather closely related.

### *Argynnis clara* Blanchard

Figure 29

BLANCHARD, 1844, p. 20 (Insects), no. 14, pl. 2, figs. 2, 3.

SPECIMEN FIGURED: Tibet, June, 1939, genitalic slide no. 277.

The male genital armature of *clara* is strikingly individual. The narrow, extremely spiculate dorsal arm is characteristic, as is the short, heavily cornute aedeagus.

### *Argynnis aglaja* (Linnaeus)

Figure 30

LINNAEUS, 1758, p. 481, no. 140.

SPECIMEN FIGURED: Darmstadt, Germany (H. Noack), genitalic slide no. 247.

This widespread and variable Palearctic species has a typically distinct genital armature, the uncus, aedeagus, and valves giving quick specific differentiation. The structure of *alexandra* Ménétriés (1832, p. 246, no. 1174) is very similar. This

latter insect should be studied to determine whether, despite pattern differences, it may not be an *aglaja* subspecies.

Speculations have been expressed that *aglaja* may be closely related to the Nearctic complex of species, if not their actual progenitor. In our judgment this is not borne out by genitalic analogies. The various offshoots in subfamily development are so genitally independent that common origins are usually beyond present demonstration. The Tertiary dispersals, fragmentations, and destructions were on so grand a scale that it is barely possible to trace interfamily lines successfully, much less to expect faithful preservation of species linkages.

### *Argynnis cydippe* (Linnaeus)

Figure 31

LINNAEUS, 1761, p. 281, no. 1066.

SPECIMEN FIGURED: "Europa," ex Eddy collection, genitalic slide no. 281, in the Museum of Comparative Zoölogy.

The similarity of *cydippe* to the three species that follow will be noted. There are close analogies in the aedeagus, the valve sclerotizations, the peculiar lyre-shaped anellus, and the heavy uncus with its tip prolongation. The present position is suggested by wing superficialities. The genitalic evidence shows only that the species are a group apart from others. No action has been taken by the present reviewers in regard to *nerippe* Felder and Felder (1862, p. 24) or *jainadeva* Moore (1864, p. 131, note), the genital armatures of which seem to resemble *cydippe* in all essential particulars. Experience has indicated that in such instances of close structural relationships a definition of the entities that may be present is impossible without an extensive knowledge of the distributions. There could well be several species represented in Asia.

### *Argynnis niobe* (Linnaeus)

Figure 32

LINNAEUS, 1758, p. 481, no. 143.

SPECIMEN FIGURED: Europe, Imhoff collection, genitalic slide no. 250, in the Museum of Comparative Zoölogy.

The genital armature resembles that of *cydippe*.

**Argynnis elisa** Godart

Figure 33

GODART, [1823], p. 817.

SPECIMEN FIGURED: Corsica, *ex* Gunder collection, genitalic slide no. 234, in the American Museum of Natural History.

This insular species is superficially distinct, but there is a close genitalic resemblance to *cydippe* and *niobe*.

**Argynnis kamala** Moore

Figure 34

MOORE, 1857, p. 156, no. 324.

SPECIMEN FIGURED: Kulu, [Punjab, India], *ex* Weeks collection, genitalic slide no. 312, in the Museum of Comparative Zoölogy.

Here is another admirable instance of the usefulness of the genital armature in pointing out relationships. The superficialities of wing pattern have occasioned the association of *kamala* with *paphia* or with various other species. The actual kinship, which is to *cydippe*, would be hard to believe were it not for the excellent genitalic affinity which is shown. The insect clearly belongs in the *cydippe* group but is specifically distinct.

**Argynnis pandora** ([Denis and Schiffermüller])

Figure 35

[DENIS AND SCHIFFERMÜLLER], 1775, p. 176.

SPECIMEN FIGURED: Sierra de Guadarrama, El Escorial, Spain, 1000 meters, June 24, 1935, genitalic slide no. 97.

The species of *Argynnis* remaining to be discussed are each genitally unique.

The short, wide, heavily serrate uncus, the distinct aedeagus, and the valves give characters for instant separation of *pandora* and subspecies.

**Argynnis paphia** (Linnaeus)

Figure 36

LINNAEUS, 1758, p. 481, no. 138.

SPECIMEN FIGURED: Darmstadt, Germany (H. Noack), genitalic slide no. 357.

The long uncus is like that of the *cydippe* group in some respects but has pronounced dorsal serrations. The heavily cornute aedeagus, the spinose bulbous dorsal arm, and the oddly recurved crista are interesting features.

**Argynnis sagana** Doubleday

Figure 37

DOUBLEDAY, 1847, pl. 21, fig. 1.

SPECIMEN FIGURED: Loutsechiang, Yunnan Province, China, genitalic slide no. 233.

The wings of the female are remarkable in that bands have replaced the usual pattern of spots. The dark color is merely an extension of the suffusion which is hinted at in related species. The wing shape, while apparently modified, is in reality unchanged except in the illusionary exaggeration that the eye receives from the arrangement of color and line. In the males, which preserve the usual *Argynnis* pattern, the genital armature is as distinct as is to be expected, although no more so than in the other unique Palearctic species. The aberrant uncus and the highly individual aedeagus are among the characters that are of interest.

**Argynnis childreni** Gray

Figure 38

GRAY, 1831, p. 33.

SPECIMEN FIGURED: Hinghwa, Fukien Province, China, October 26, 1921, genitalic slide no. 297, in the American Museum of Natural History.

This insect, the largest and most magnificent in the subfamily, is likewise genitally so distinct that the figure obviates comment.

**Argynnis anadyomene** Felder and Felder

Figure 39

FELDER AND FELDER, 1862, p. 25.

SPECIMEN FIGURED: Kanagawa, Japan (Gulick), genitalic slide no. 321.

The valve sclerotizations differ in detail, although the dorsal arm is distally swollen and spinose as in some other species. The upcurved, simple uncus and the distinct aedeagus give complete specific separation.

**Argynnis niphe** (Linnaeus)

Figure 40

LINNAEUS, 1767, p. 785, no. 208.

SPECIMEN FIGURED: Chunking, W[est] China, September 17, 1919, genitalic slide no. 231.

By reason of wing pattern differences and because of the tropical distribution, *niphe* has been regarded as hovering on the verge of unrecognizability as an *Argynnis*.

In genital armature apparently it is no more modified than are the other species grouped here. The distal extension of the cucullus is remarkable but the remainder of the armature, although very distinct, is of the *Argynnis* type.

### **Argynnis laodice** (Pallas)

Figure 41

PALLAS, 1771, p. 470.

SPECIMEN FIGURED: Kirin Province, Manchuria, August 3, 1937 (Wing), genitalic slide no. 320.

### **Argynnis lysippe** Janson

Figure 42

JANSON, 1877, p. 154.

SPECIMEN FIGURED: Venoshibe, n[ea]r Sakai, Nippon, July 14, 1937 (Yano), genitalic slide no. 279.

It is interesting to note in the literature how various authors have spoken, now of this species and now of that, as having but dubious placement in *Argynnis*, although *laodice* and *lysippe* seldom attract this degree of attention. In our judgment they are the most pronouncedly divergent species found in all the array of genitalic variations examined. The odd tegumen, weird aedeagus, fluke-shaped anellus, and modified valves seen in these two species preclude further association to other argynids. The two, although similar and related, are completely distinct in detail, the valves and the aedeagus of each making identification very easy.

### **SPEYERIA** SCUDDER

*Speyeria* SCUDDER, 1872, p. 23. GENOTYPE: *Nymp. phal. idalia* Drury, [1773], Index to vol. 1, p. 25, pl. 13, figs. 1-3. FIXATION: Original designation monotypic.

*Semnopsyche* SCUDDER, 1875b, p. 258. GENOTYPE: *Papilio diana* Cramer, [1777], vol. 2, p. 4, pl. 98, figs. D, E. FIXATION: Original designation monotypic.

All of the Nearctic species that have been classified under *Argynnis* are herein considered to belong in a distinct genus for which the name *Speyeria* is available. It is impossible to deny that certain Palearctic groups (those having the *cydippe* type of genital armature, for one example) logically should be given generic status also. No attempt has been made to classify the

Palearctic species. We are content that the Old World workers decide their own needs, but we wish to give the Nearctic species the generic recognition to which they seem entitled.

The genus *Speyeria* is confined to North America, as far as we have been able to ascertain, with no close relatives upon the other continents. None of the species resemble *paphia* (the genotype of *Argynnis*) in genitalic structure. A generic character for *Speyeria* is found in the dorsal arm which is a semirectangular plate so distinct in form that a separate term has been used in speaking of it (digitus, fig. 54). The remainder of the armature of *Speyeria* is more conventional in type and is comparatively unspecialized. The anellus is simple, only very slightly varied in form throughout the genus, the valves differ but little, and the aedeagus as well as the uncus is relatively similar in all species. Upon the basis of the male armature, *Speyeria* is singularly homogeneous, although a division that can be made upon evidence of difference in the female armature will be described below.

### **Speyeria callippe** (Boisduval)

Figure 43

BOISDUVAL, 1852, p. 302.

SPECIMEN FIGURED: Oakland, California, June 12, 1940 (R. J. Wind), genitalic slide no. 328.

Since it is the oldest name, *callippe* is figured to represent a group of Nearctic species which have not yet been found separable by genitalic differences. The species *atlantis* (figs. 52, 54) belongs in this group. The uncus tapers gently to a simple, ventrally curved tip. The digitus is not greatly extended, and the aedeagus is extensively cornute, as in all *Speyeria*. Lest variable details receive too serious attention, it should be emphasized that conclusions will be very unreliable unless based upon extensive material. Oftentimes, a few preparations will seem to show distinctions, which are nullified when more specimens of a given population are examined, and this is even more true of comparisons extended to involve the various subspecies of a major distribution. The foregoing remarks should not be construed

as raising doubts about the actual validity of species other than those which separate genitally, even though the other groups in the subfamily do appear to be subject in large degree to genitalic separation. It is well known that distinguishing characters may be found among species that are genitally similar, as in this present instance where the species definitions must await an exhaustive marshalling of ecological data which are not within the scope of the present survey.

### *Speyeria edwardsii* (Reakirt)

Figure 44

REAKIRT, 1866, p. 137.

SPECIMEN FIGURED: R[ocky] M[ountain] N[ational] P[ark], Colorado, July 21, 1931, genitalic slide no. 324.

This species is the most instantly separable genitally of the species of *Speyeria*, having in the males a very narrowed and extended digitus. The process is five or six times as long as its breadth, a notable extension since the other species seldom have a digitus more than three times as long as its width. The uncus tapers gently to a claw-like terminus as it does in the large group of which *callippe* is typical.

### *Speyeria idalia* (Drury)

Figure 45

DRURY, [1773], Index to vol. 1, p. 25, pl. 13, figs. 1-3.

SPECIMEN FIGURED: Butler County, Pennsylvania, July 4, 1939 (F. Chermock), genitalic slide no. 343.

This gorgeous insect is distinctive in the male genital armature, although the departure from typical structure is comparatively insignificant and merely of specific value. There can be but little question that *Speyeria* is applicable to the whole Nearctic group, since all of the species agree well in morphology with *idalia* upon which *Speyeria* was founded. The aedeagus presents some modifications, and the outline of the digitus in its distal extension is also constantly indicative of the species. The subterminal ventral excavation in the uncus outline, with only minor variations, is common to *idalia* as well as to the species that follow.

### *Speyeria nokomis* (Edwards)

Figure 46

EDWARDS, 1862b, p. 221.

SPECIMEN FIGURED: Round Valley, California, August 4, 1931, genitalic slide no. 326.

Although fairly adequate genitalic distinction is apparent, the characters are minor, to be observed only with close comparative study of series and fully valid only because of their cumulative weight. From *diana*, the species that is closest in point of superficial resemblance, there is positive separation so we know beyond doubt that there can be no possibility of an East-West association in the replacement sense; each is a valid entity. In fact, *nokomis* allies closer with *idalia*, *edwardsii*, and the *callippe* group of species than with *diana*. In the female genital armature, *nokomis* has a simple bursa copulatrix as do the other species of *Speyeria* previously discussed. (Cf. fig. 52, dorsal view of terminal outline, bursa of *atlantis*, typifying the condition prevailing in the species discussed so far.)

### *Speyeria diana* (Cramer)

Figure 47

CRAMER, [1777], vol. 2, p. 4, pl. 98, figs. D, E.

SPECIMEN FIGURED: Gastonia, North Carolina, June 13, 1937 (R. McKenzie), genitalic slide no. 323.

In the male the digitus is characteristic, widening distally by reason of an abrupt ventral angle which in this exact outline is peculiar to *diana* alone. The female bursa is extended by a narrow, tubular connection to a secondary membranous pouch which is long oval in outline and comparatively small. This secondary bursa, along with other features common to the genital armature of both sexes, gives ample evidence that *diana*, *cybele* (Fabricius) (1775, p. 516, no. 311), and *aphrodite* (Fabricius) (1787, vol. 2, p. 62, no. 590) comprise a closely related group. There is some relationship to *nokomis* and *idalia*, seen in the male uncus, although by comparison of the females the two latter species go with *edwardsii* and the *callippe* complex.

This bursal separation should be given due weight since probably it is the most important structural difference to be found among the species of *Speyeria*. Should

future reviewers adopt an elaborate classification of the argynnids, *Semnopsyche* could hardly fail to be listed as an independent genus for the species which have a secondary bursa (*diana*, *cybele*, and *aphrodite*).

**Speyeria cybele** (Fabricius)

Not figured

FABRICIUS, 1775, p. 516, no. 311.

**Speyeria aphrodite** (Fabricius)

Figures 48, 53

FABRICIUS, 1787, vol. 2, p. 62, no. 590.

SPECIMEN FIGURED: Butler, Pennsylvania, July 24, 1939 (F. Chermock), genitalic slide no. 344.

No figure of *cybele* has been given since the genital armature is so similar to *aphrodite* that constant characters of separation have not been found. Oftentimes, local populations can be identified by careful attention to minor points of variation in the male sex organs and by the difference in characteristic outline of the female bursae, yet, when applied against the whole known range, these are slight and poorly defined differences merely in degree, which have not been accepted as wholly reliable. The best possible morphological separation of these two species continues to be found in the male sex scaling on the veins of the primaries. This is very heavy in *cybele* and its western replacements, while *aphrodite* has the lightest vein scaling observed in any of the species of *Speyeria*. This is constant throughout the range and hence an unailing character by which all of the subspecies of *aphrodite* and *cybele* may be separated. Attention is called to figures 52 and 53, outlining the dilated female bursae of *atlantis* and *aphrodite*, the contrast showing the *Semnopsyche* group as being distinct from all other related species in North America. (Before the glycerin to water transfer the difference is even more pronounced, since the tubular connection between bursae is much smaller before dilation, and the two bursal sacs are then very distinctly separated.)

**Euptoieta DOUBLEDAY**

*Euptoieta* DOUBLEDAY, 1848, p. 168. GENOTYPE: *Papilio claudia* Cramer, [1775], vol. 1, p. 109, pl. 69, figs. E, F. FIXATION: Scudder, 1872, p. 22.

We feel under no obligation to work upon this genus. The species of *Euptoieta* are incongruous by venation and by genital armature with Argynninae, being one of several aberrant groups linking to Heliconiinae. Perhaps the dorsal sclerotization upon the male uncus is a generic character; however, the names were not all investigated. The rarer South American representatives should be easy to define as independent species or as subspecies of the two most important, widely distributed, well-known, and genitally very distinct entities that follow.

**Euptoieta claudia** (Cramer)

Figure 49

CRAMER, [1775], vol. 1, p. 109, pl. 69, figs. E, F.

SPECIMEN FIGURED: Sand Ridge, Manitoba, August 4, 1935 (J. May), genitalic slide no. 333.

In the valve of the male genital armature, the dorsal process extends to an odd, paw-shaped appendage which bears five long spines and several shorter ones. The anellus is in the form of a Y, with spoon-shaped lobes upon the two upright arms. The aedeagus is distally swollen in outline, roughly bell-shaped in terminus. This short, compressed, and distally enlarged organ is very distinct from the longer, straighter, and more slender aedeagus of the species that follows. The sclerotized bridge upon the dorsum of the uncus is probably specifically distinct in shape.

**Euptoieta hegesia** (Cramer)

Figure 50

CRAMER, [1779], vol. 3, p. 30, pl. 209, figs. E, F.

SPECIMEN FIGURED: Mapastepec, Mexico, June, 1939 (D. B. Stallings), genitalic slide no. 332.

The uncus is well differentiated from that seen in *claudia*, both in typical outline and in sclerotized dorsal armature. The valves have a similar, paw-shaped dorsal appendage which is smaller, with fewer and much shorter spines. The anellus lobes, extending from a U-shaped formation, are more delicate in sclerotization. The aedeagus will provide diagnosis, as noted above, when contrasted with that organ in *claudia*.

## DISCUSSION

It is fortunate that Warren's revision of *Boloria* (1944) was published in time for us to add a short review and a comparison with our views. There has been no exchange of data or collaboration between us; our paper was nearly completed before we learned of his studies. Also, we were unable to follow comprehensively the involved and scattered papers of Reuss. (Warren has performed a notable service in assembling and interpreting Reuss' work.) The fact is, then, that three fully independent genitalic studies of Argynninae have been conducted. Hence, those critics who may be inclined to doubt the value of a genitalic approach to problems of relationship among species and genera should find it interesting to compare the results separately achieved. Instead of summarizing here our present paper, we shall attempt a review of whatever we find of agreement or of disagreement in the conclusions of Reuss, Warren, and ourselves.

Between Warren and Reuss there are some differences in terminology and some disagreements concerning the validity of certain generic names, but there is an impressive similarity of opinion concerning the relationships. In comparison with Warren's revision our present survey differs somewhat in the use of genitalic terms. (We have followed the common usages of American students or have coined descriptive words and phrases where applicable names seemed lacking.) The genitalic groups separated or indicated as distinct by us coincide almost exactly with those recognized by Warren, even, in a number of instances, to exact sequence of species. We have approximately the same ideas of generic sequence. Allowing for some inevitable differences in usage and opinion, the agreement in these separate investigations confirms the validity of certain of the outstanding inferences shared in common.

The most important of these generalizations is that the close similarity of wing pattern throughout Argynninae is a subfamily (not a generic) characteristic. These similar appearing insects have been

found to be separable by many structural differences. In view of the uncertainty of past workers as to the limits of *Argynnis* and *Brenthis* (unrestricted), this alone is a startling discovery. Warren believes that the genera are rather widely separate, in an evolutionary sense, and follows Reuss in exploiting the genitalic differences to the fullest. This results in the recognition of numerous small genera, especially for the Palearctic species, which are seen to differ so greatly in genital armature.

In formulating a genitalic separation, Warren (1944, p. 6) follows Reuss in stating that the following characters are "... common to all species of Argynnids and peculiar to them: (1) the presence of a non-chitinised area in the dorsal region of the 9th tergum, and (2) the fact that the terminal (distal) process of the harpe lies external to the clasper." (In comparison of descriptions Warren's term "head of the harpe" applies to the dorsal process termed "valvenflagellen" by Reuss and "dorsal arm" by us. Warren further considers that the dorsal lobe, the crista, and the dorsal arm, as we use the terms, compose the "harpe" as distinct from the claspers, or lower portion of the valve.)

As far as we have been able to check them, these structural peculiarities will go far toward isolating Argynninae. We recently investigated *Basilarchia*, finding it to be fully distinct and not at all an argynnid type. However, *Euptoieta* proves to be curiously intermediate, as we have observed heretofore. The tegumen does not have the dorsal membranous area, but the dorsal process of the valve is analogous to *Argynnis* in situation. Thus, the position of *Euptoieta* is probably approximately as we have placed it. We believe that we are correct in concluding that the subfamily most nearly related to Argynninae is Heliconiinae, with a few traces of persisting structural linkage. Therefore, aside from the possibility of a very few intermediate American species, the genitalic features of the membranous area located dorsocentrally on the tegumen and the dorsal process exterior to the lower

portion of the valve should prove to be faithfully diagnostic for the present subfamily. Warren agrees that the *Melitaea* group of genera are not to be associated with Argynninae.

As to the details of a classification for the Palearctic argynnids, we repeat that we are content that the Old World workers decide their own needs. For the convenience of American students who may not have access to Reuss' and Warren's papers, we give an outline of the genera they use, as listed by Warren (1944, pp. 26-30).

*Issoria* Hübner for *lathonia*, *gemma*, and the African species.

*Fabriciana* Reuss (1920, p. 192) for the species we termed the *cydippe* group. Reuss designated *Papilio niobe* Linnaeus as the genotype.

*Neoacidalia* Reuss (1926a, p. 69) for "... according to Reuss (1926), four Asiatic and thirty-four American species." Reuss designated "*Papilio cybele* Cramer" [*sic*] as the genotype.

*Mesoacidalia* Reuss (1926a, p. 69) for the designated genotype *aglaia*, also *alexandra* and related species, with *clara* placed in subgenus *Proacidalia* Reuss (1926a, p. 69).

*Argynnis* Fabricius for *paphia*.

*Pandoriana* Warren (1942, p. 246) for *pandora*, with genotype designated as *Papilio maja* Cramer ([1775], vol. 1, p. 39, pl. 25, figs. B,C) (= *pandora* [Denis and Schiffermüller]).

*Childrena* Hemming (1943, p. 30), a new name for the homonym *Eudryas* Reuss (1926b, p. 253) for *childreni*, the designated genotype.

*Argyreus* Scopoli for *niphe*.

*Damora* Nordmann for *sagana*.

*Argynome* Hübner for *laodice*.

We venture no comment upon the purely Palearctic classification other than to point out that we arrived at an extremely similar grouping and arrangement of groups. We agree that *Issoria* and *Fabriciana* are ancient and suggest that in a world list *Speyeria* might well follow *Issoria* and precede *Fabriciana*, also that the South American species may comprise a genus which should head such a list. Of course, there is no actual kinship shown other than that in the argynnids these

groups agree in the relative simplicity of genitalic structure; also, the dispersals correlate with what is known of certain Tertiary mammalian distributions, giving basis for speculation that these genera had early distinctness.

We do not see how *Neoacidalia* Reuss can apply to any American species. By genitalic limitations the only recognizable Nearctic groups fall under Scudder's prior names, i.e., *Speyeria* and *Semnopsyche*. Any genus with *cybele* as its genotype would be a synonym of *Semnopsyche* with genotype *diana*. The similar armature in all Nearctic species raises doubts if generic elaboration is called for. We know of no Asiatic *Speyeria*.

Warren follows Reuss in limiting *Brenthis* Hübner to the *hecate* group with exactly the same species and the same generic characters mentioned by us. This restriction of *Brenthis* is a necessity and must stand, however greatly workers may deplore the change in long-established usage. Its retention in a wider sense would be to continue a grave error in associations.

Warren's monograph proper is concerned only with *Boloria* Moore which he restricts to the *pales* group. He distinguishes three species, genitally separable, in the forms hitherto associated with *pales*, and asserts that the Nearctic races fall under *napaea* Hoffmansegg (1804, p. 196). In his review of genera he has placed *aphirape* in the genus *Proclassiana* Reuss<sup>1</sup> (1926a, p. 69) and all of the remaining species herein listed as *Boloria* under *Classiana* Reuss.

We believe that this treatment of *Boloria*, *Proclassiana*, and *Classiana* is open to some difference of opinion. We realize that the staggering task of revising the world species which Reuss and Warren place in *Classiana* may be delayed for many years, and in the meantime data essential to a final estimation of the subfamily are missing. Hesitancy is further prompted by the fact that an intensive study of the female armature in Argynninae might do much toward deciding if the variation in the male genital armature

<sup>1</sup> Warren has asked us to point out that his reference to the original description of this genus is not correct.



can be used alone as a basis for generic separations. Some allowances might have to be made if a series of uniformities in the former sex were found. If the arguments for numerous small genera, amply documented by three independent genitalic surveys of the males, were further borne out by characters in the genitalic armature of the females, the conclusions of Reuss and Warren could hardly fail to be accepted. Pending further data we see no reason why the name *Boloria* cannot be used in a loose sense by American students to replace the name *Brenthis* which has been lost to the Palearctic fauna. Specialists may wish to use the several restricted genera, but in our opinion *Clossiana* contains a genitalic diversity in which there are groups comparable in value to *Boloria* (restricted) and *Proclossiana*. Apparently, still more genera will be required if Reuss' concepts are to prevail.

All of the species that we placed in *Boloria* agree in possessing the bifid uncus and the basally closed aedeagus. The latter feature was not emphasized by Warren because, he says (*in litt.*), it is found in other Lepidoptera. Still, within the

present subfamily it is remarkable and may be used along with the bifid uncus and simple valve as a character by which *Boloria* is distinct from all other argynnids, including *Brenthis*. An integrating category, not expressed by the several genera in the concepts of Reuss and Warren, would be justified because of likenesses seen throughout *Boloria* (unrestricted). We agree with those authors that in propounding a classification for Argynninae the great diversity in male genital armature should be considered. However, it would seem essential not to lose sight of gross differences and similarities while pointing out the special characters of species and species groups. Until further data are secured, differences in opinion may be allowed, our opinion being that the invariable similarity of structure of the aedeagus would alone justify the use of subgenera under *Boloria* rather than to recognize several restricted genera. The isolation of groups which is implied by the latter classification may be close to the truth in an evolutionary sense, but the fact of genitalic similarity weighs against the variation which is found.

#### CONCLUSION

By this survey and by what has been said concerning the views of Reuss and Warren, American students of Argynninae will see that *Brenthis* and *Argynnis* should be restricted to Palearctic species. The genitalic peculiarities of *Brenthis* set it apart from the Holarctic species for which the name *Boloria* (unrestricted) is available. In *Boloria*, the bifid uncus and basally closed aedeagus provide genitalic characters for a basic separation. For many of the species there are nomenclatorial and distributional problems, involved through circumpolar dispersals, complicating the difficulties of morphological studies which are needed before final estimations can be made of classificational requirements. Perhaps *Boloria* will require several genera or subgenera, along lines indicated by Reuss. The primary separation from other major groups in Argynninae may be said to be complete and satisfactory. The group of

larger species usually termed argynnids are found to be greatly varied in genitalic structure. Specialists concur upon the desirability of recognizing numerous genera. Among these genitally isolated groups, *Speyeria* has outstanding peculiarities which are shared by all Nearctic species. It has been demonstrated that the prevailing uniformity of wing pattern in the subfamily is wholly unusable as an indicator of generic relationships. The genitalic distinctness of *Speyeria* as compared to *Argynnis* gives ample warrant for the generic separation and is yet another in a series of proofs of the evolutionary gulfs separating the genera in Argynninae. With the isolated position of *Speyeria* thus demonstrated, it is obvious that revisional studies of Nearctic species may proceed without need of further reference to species upon other continents.

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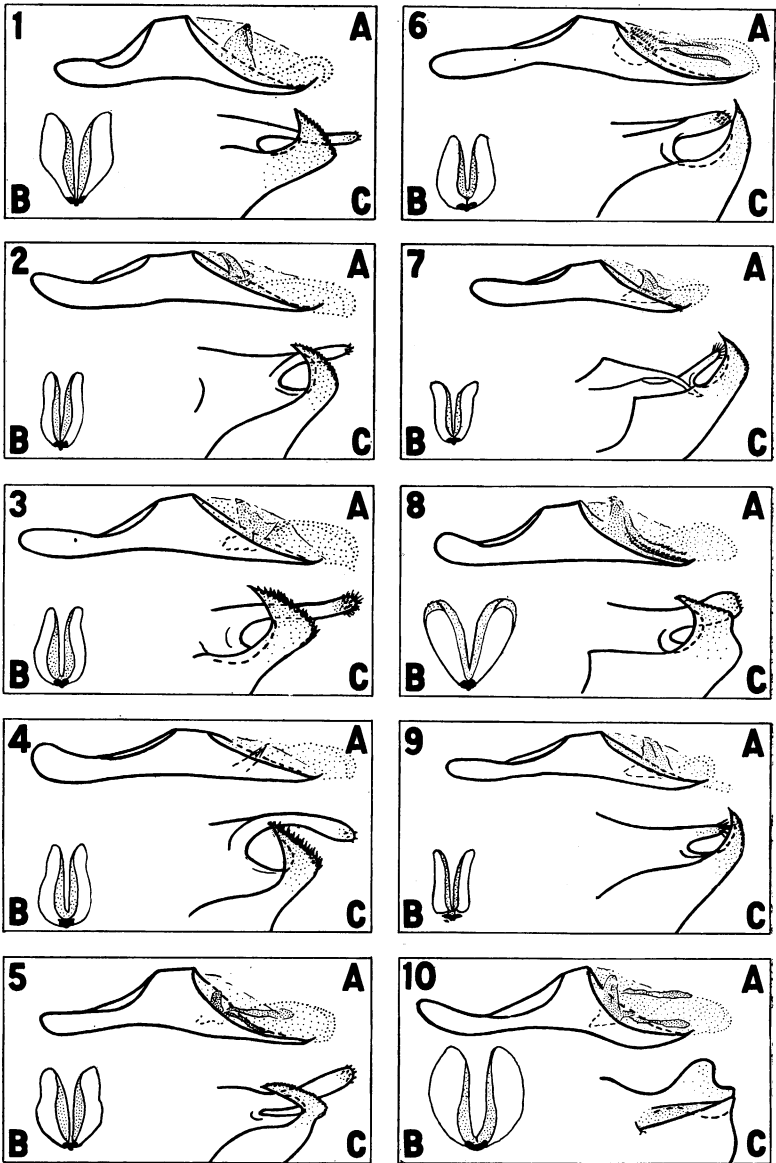
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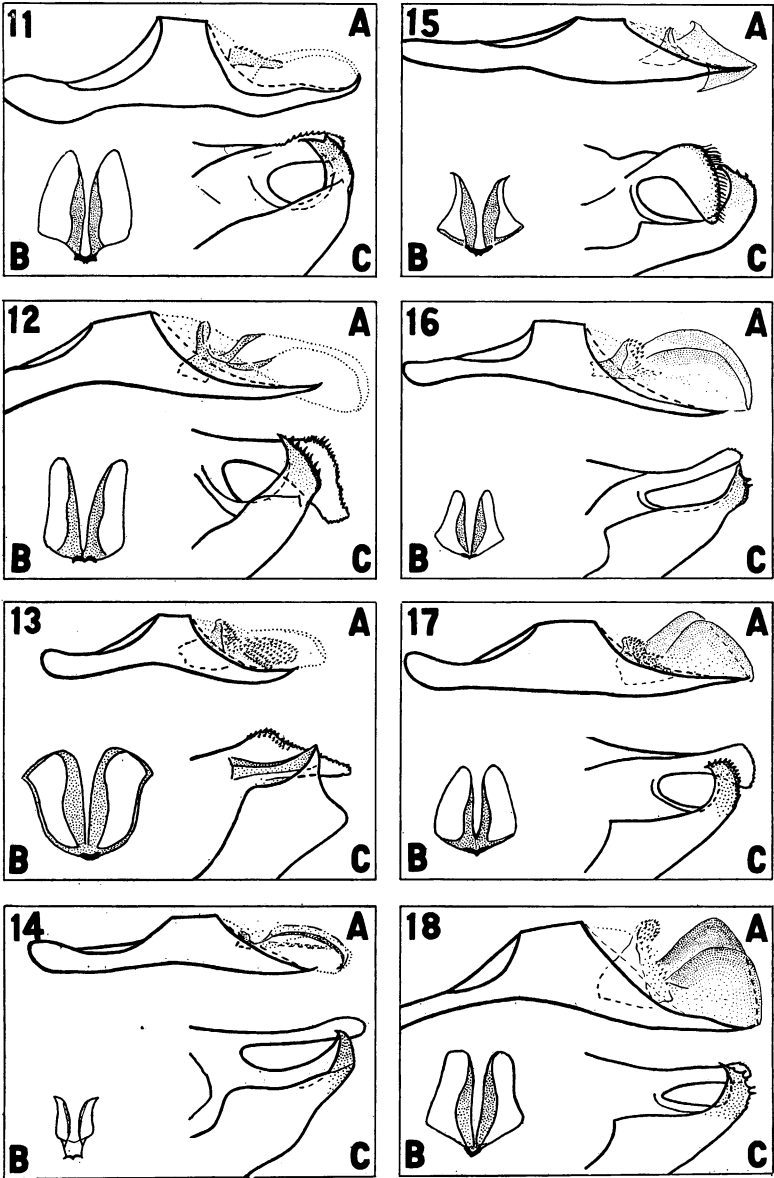
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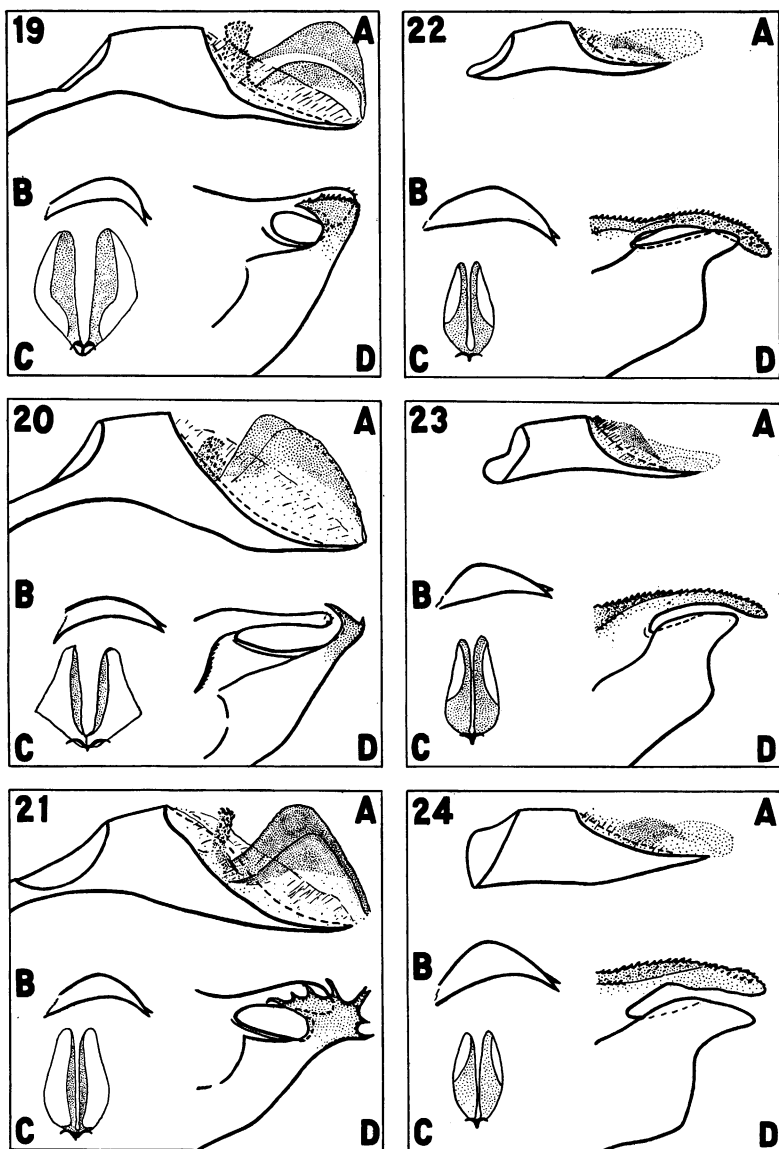
1840. Insecta Lapponica. Leipzig, Leopold Voss, vi+1140 pp.



Figs. 1-10. Male genitalia, *Boloria*. A, Aedeagus; B, anellus; and C, valve terminalia of (1) *thore*, (2) *improba*, (3) *frigga*, (4) *toddi*, (5) *selene*, (6) *polaris*, (7) *jerdoni*, (8) *gong*, (9) *haberhaueri*, (10) *aphirape*. Enlarged about 22 $\times$ .

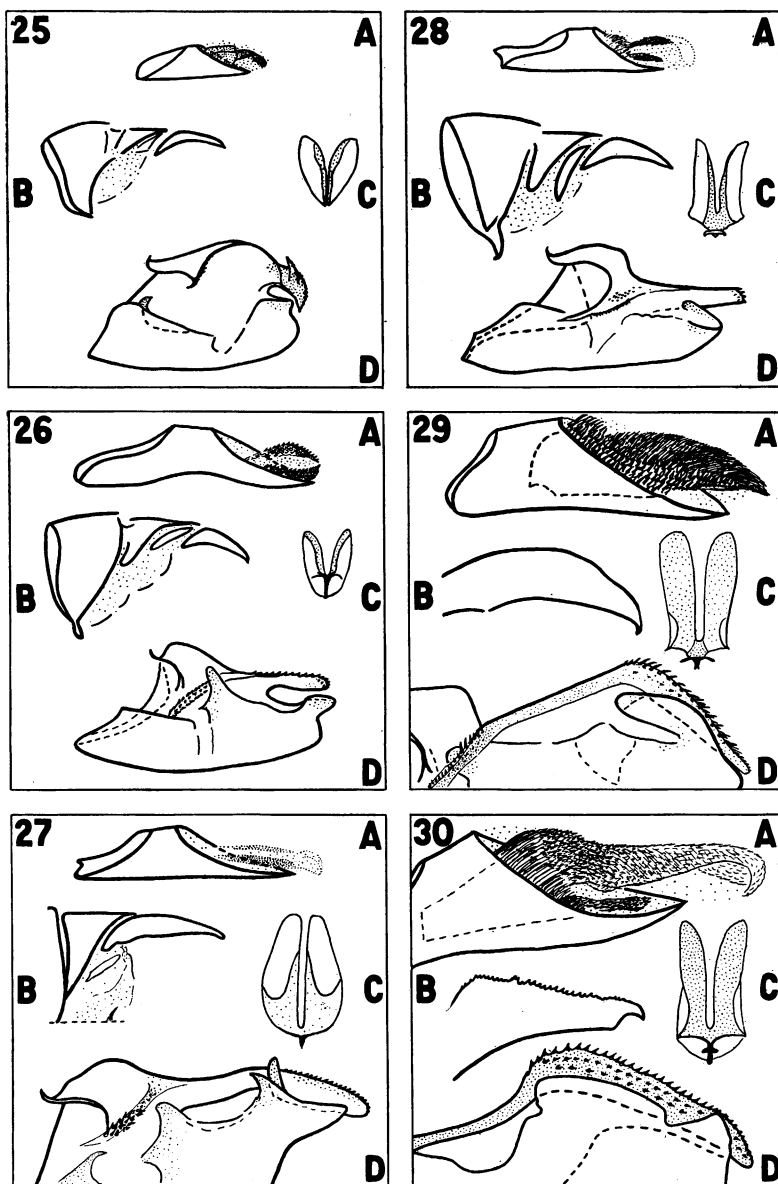


Figs. 11-18. Male genitalia, *Boloria*. A, Aedeagus; B, anellus; and C, valve terminalia of (11) *alberta*, (12) *amphilochus*, (13) *pales*, (14) *dia*, (15) *freija*, (16) *selenis*, (17) *euphrosyne*, (18) *chariclea*. Enlarged about 22 $\times$ .

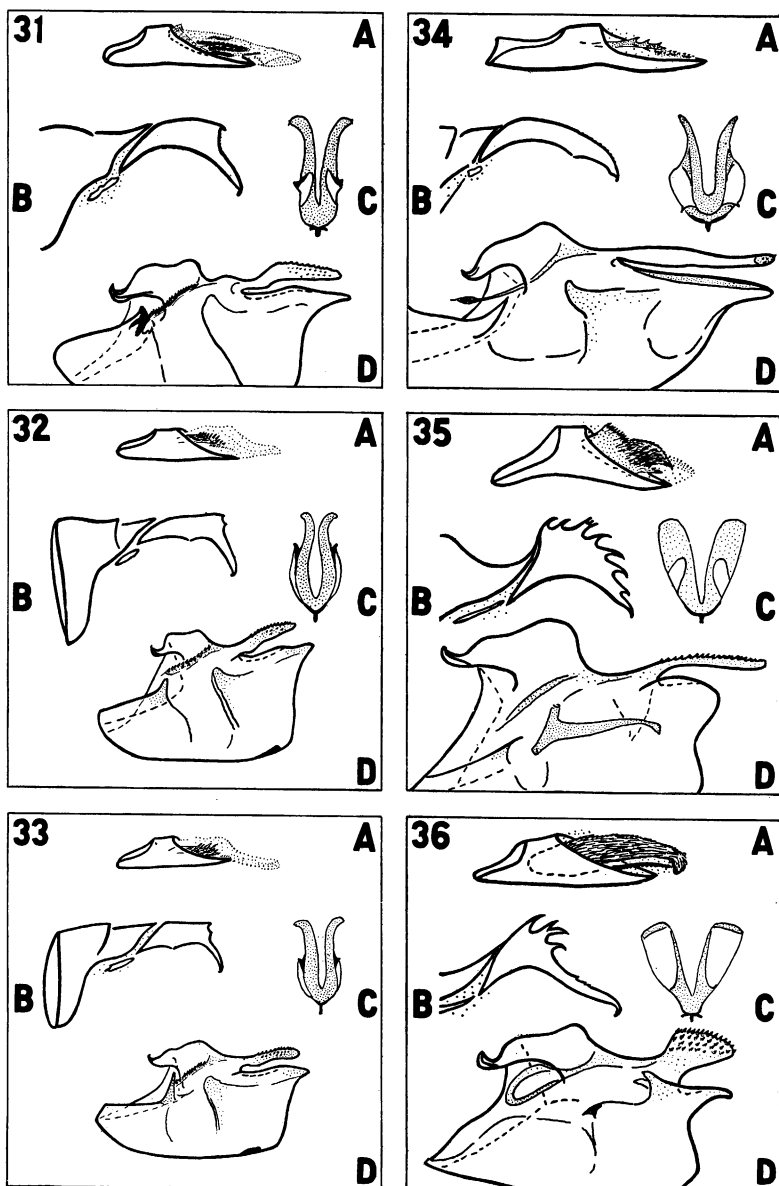


Figs. 19-24. Male genitalia, *Boloria* and *Brenthis*. A, Aedeagus; B, uncus; C, anellus; and D, valve terminalia of (19) *Boloria rossicus*, (20) *oscarus*, (21) *angarensis*, (22) *Brenthis hecate*, (23) *ino*, (24) *daphne*. Enlarged about 22 $\times$ .

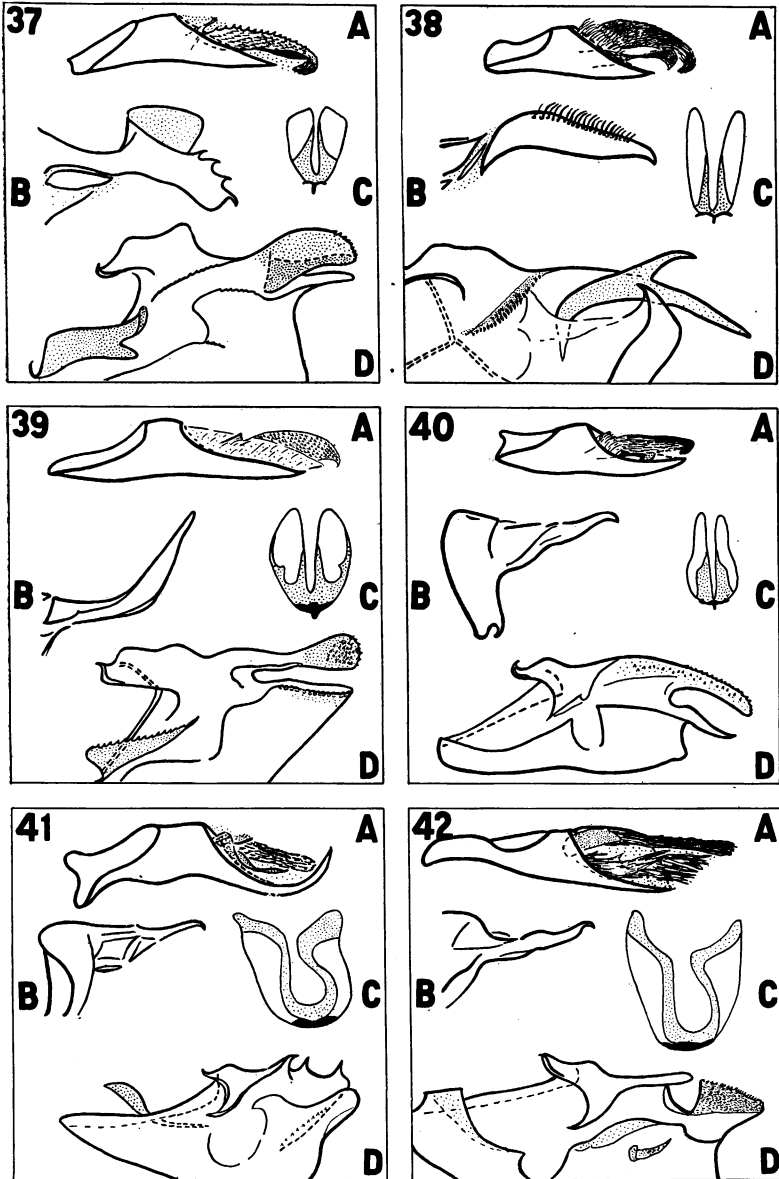




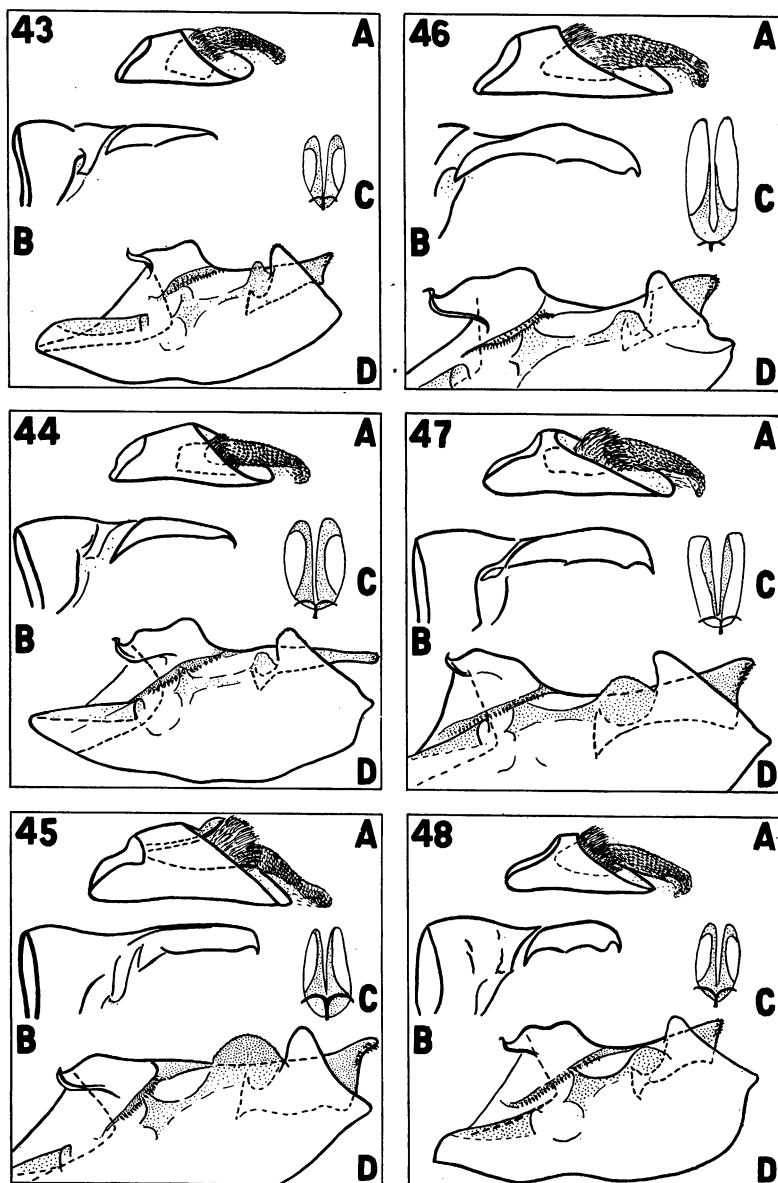
Figs. 25-30. Male genitalia, *Argynnis*. A, Aedeagus; B, uncus; C, anellus; and D, detail of valve of (25) *cytheris*, (26) *hanningtoni*, (27) *lathonia*, (28) *gemmata*, (29) *clara*, (30) *aglaia*. Enlarged about 22X.



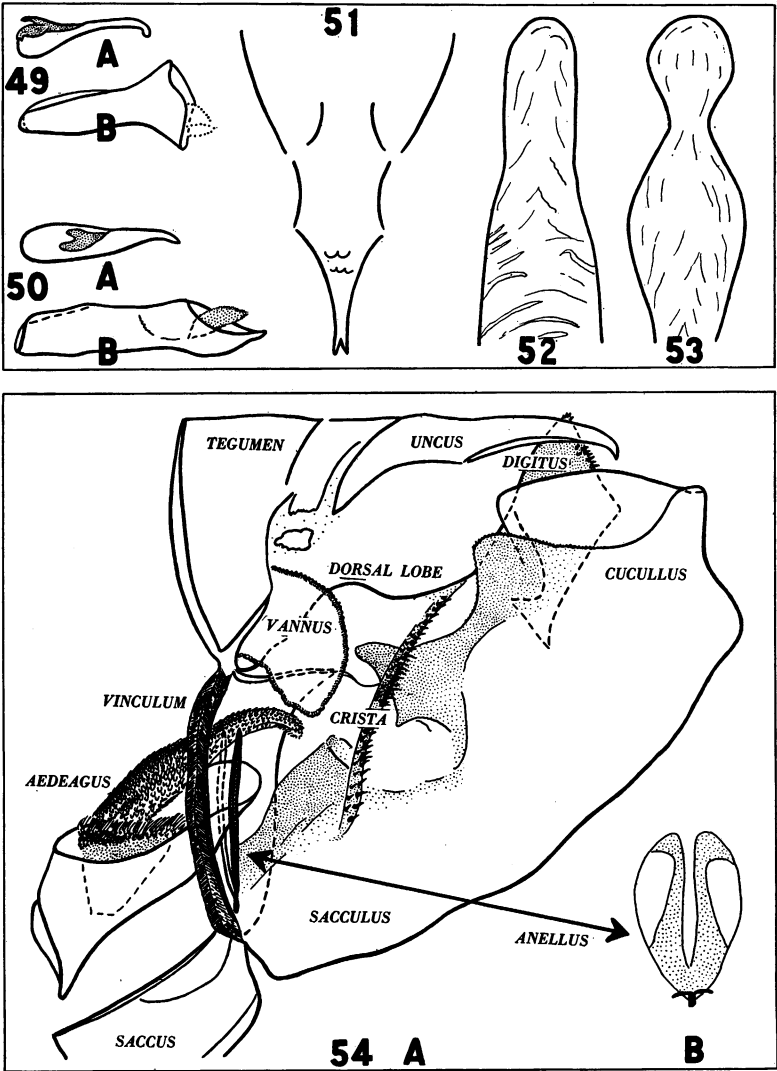
Figs. 31-36. Male genitalia, *Argynnis*. A, Aedeagus; B, uncus; C, anellus; and D, detail of valve of (31) *cydippe*, (32) *niobe*, (33) *elisa*, (34) *kamala*, (35) *pandora*, (36) *paphia*. Enlarged about 11X.



Figs. 37-42. Male genitalia, *Argynnis*. A, Aedeagus; B, uncus; C, anellus; and D, detail of valve of (37) *sagana*, (38) *childreni*, (39) *anadyomene*, (40) *niphe*, (41) *laodice*, (42) *lysippe*. Enlarged about 11X.



Figs. 43-48. Male genitalia, *Speyeria*. A, Aedeagus; B, uncus; C, anellus; and D, detail of valve of (43) *callippe*, (44) *edwardsii*, (45) *idalia*, (46) *nokomis*, (47) *diana*, (48) *aphrodite*. Enlarged about 11X.



Figs. 49-54. Genitalia of Argynnninae. A, Uncus, and B, aedeagus of (49) *Euptoieta claudia* and (50) *Euptoieta hegesia*; dorsal view of uncus of (51) *Boloria selene*; dilated bursal terminalia, females of (52) *Speyeria atlantis* and (53) *Speyeria aphrodite*; lateral view of the left side, left valve removed, full male armature of (54A) *Speyeria atlantis* with terminology used and (54B) separate cephalad view of anellus, the arrow pointing to its lateral position when *in situ*. Enlarged about 22X .

