This study began as an effort to determine the validity of the subspecies name *nebraskensis* (Holland) as applied to *Boloria selene* (Denis & Schiffermüller) populations in a limited area of southeastern Nebraska. As the study progressed, it became evident that the eastern limit of the range of *nebraskensis* was not known and that the relationship of *nebraskensis* to *myrina* (Cramer) was not well understood in the published literature. It also was apparent that considerable variation in both size and markings was present within the described subspecies of *selene* and that a considerable amount of intergradation occurred in some geographic areas between the populations traditionally considered as subspecies of *selene*. For these reasons, the study was expanded to include the entire range of *B. selene* in North America (Fig. 1).

The North American subspecies of *selene* were formerly placed under the species *myrina* in the genus *Brenthis* Hübner (McDunnough, 1938). Clark (1941) recognized that *myrina* and the European *selene* were conspecific and placed the North American subspecies under *selene*. Studies of male genitalia by dos Passos & Grey (1945) reinforced Clark's placement of *myrina* under *selene*. These studies showed that all the North American representatives of the genus *Brenthis*, including *selene*, should be placed in the genus *Balaria* Moore.

The populations considered subspecies of *selene* actually represent aggregations of populations homogeneous in wing characters but on a larger scale representing the distinct clustering of characters amid broad clines. Subspecies names are valuable in characterizing these groups as to phenotypic appearance, habitats, and ecological-range affinities. Subspecies names are used in this paper for these reasons.

A total of 1,264 specimens, representing all of the named subspecies, was obtained from museum and private collections for examination. This paper presents the results of the study of these specimens, integrated with previous knowledge of the species. Seven subspecies are recognized.

**Methods.** Characters used to differentiate the subspecies of *selene* are given in Tables 1 and 2. The degrees of dorsal maculation, dark dorsal
Table 1. Comparison of characters of the North American subspecies of *Boloria selene*.

<table>
<thead>
<tr>
<th>Character</th>
<th>myrina</th>
<th>nebraskensis</th>
<th>sabulocollis</th>
<th>tollandensis</th>
<th>albequina</th>
<th>atrocostalis</th>
<th>terrae-novae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of typical specimens examined</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>130</td>
<td>232</td>
<td>51</td>
<td>88</td>
<td>15</td>
<td>159</td>
<td>14</td>
</tr>
<tr>
<td>Females</td>
<td>63</td>
<td>166</td>
<td>8</td>
<td>53</td>
<td>6</td>
<td>80</td>
<td>1</td>
</tr>
<tr>
<td>FW length, mm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>20.98</td>
<td>24.78</td>
<td>22.82</td>
<td>19.55</td>
<td>19.17</td>
<td>20.08</td>
<td>20.67</td>
</tr>
<tr>
<td>Females</td>
<td>21.85</td>
<td>25.73</td>
<td>23.75</td>
<td>20.46</td>
<td>20.08</td>
<td>20.57</td>
<td>21.50</td>
</tr>
<tr>
<td>Degree of maculation (dorsal)</td>
<td>2.29</td>
<td>1.99</td>
<td>1.82</td>
<td>1.50</td>
<td>2.33</td>
<td>2.25</td>
<td>2.33</td>
</tr>
<tr>
<td>Degree of dark marginal wing scaling (dorsal)</td>
<td>1.52</td>
<td>1.14</td>
<td>1.80</td>
<td>1.22</td>
<td>3.00</td>
<td>3.19</td>
<td>1.93</td>
</tr>
<tr>
<td>Degree of dark basal wing scaling (dorsal)</td>
<td>1.70</td>
<td>.87</td>
<td>1.20</td>
<td>2.14</td>
<td>4.33</td>
<td>2.10</td>
<td>2.47</td>
</tr>
<tr>
<td>Percentage of specimens with basal spot in discal cell of dorsal HW obscured</td>
<td>30</td>
<td>6</td>
<td>15</td>
<td>79</td>
<td>100</td>
<td>60</td>
<td>93</td>
</tr>
<tr>
<td>Percentage of specimens with anvil-shaped silver spot in cell Cu₂ of ventral HW divided</td>
<td>12</td>
<td>4</td>
<td>4</td>
<td>30</td>
<td>33</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>Yellow scaling invading cinnamon color of basal and discal areas of ventral HW²</td>
<td>++</td>
<td>++</td>
<td>+++</td>
<td>+++++</td>
<td>+++++</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

¹Values represent an average obtained by visually rating each specimen on a scale of 0–5.
²Average appearance of each subspecies based on a composite of all specimens examined.

Marginal wing scaling, and dark basal wing scaling dorsally, given for each subspecies, represent averages of numerical values obtained by visually rating each specimen on a scale of zero to five. The values for the amount of yellow scaling that invades the cinnamon color of basal and discal areas of the ventral HW (hindwing) represent the average appearance of each subspecies based on a composite of all specimens examined. These are also on a scale of zero to five. Division of the anvil-shaped silver spot in cell Cu₂ of the ventral HW is not intended to be a main character for separation of subspecies. It is used to point out the close relationship of *albequina* (Holland) to *tollandensis* (Barnes & Benjamin).
Table 2. Comparison of width to height ratios\(^1\) of median black lunules in cells Rs, M\(_1\), M\(_2\), M\(_3\), and CU\(_1\) of the ventral FW of some North American *Boloria selene* subspecies.

<table>
<thead>
<tr>
<th></th>
<th>myrina</th>
<th>nebraskensis</th>
<th>sabulocollis</th>
<th>tollandensis</th>
<th>atrocostalis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of specimens examined</td>
<td>116</td>
<td>127</td>
<td>59</td>
<td>44</td>
<td>66</td>
</tr>
<tr>
<td>Cell Rs</td>
<td>1.34</td>
<td>1.37</td>
<td>1.38</td>
<td>1.20</td>
<td>1.32</td>
</tr>
<tr>
<td>Cell M(_1)</td>
<td>1.27</td>
<td>1.38</td>
<td>1.25</td>
<td>1.22</td>
<td>1.17</td>
</tr>
<tr>
<td>Cell M(_2)</td>
<td>1.58</td>
<td>1.70</td>
<td>1.49</td>
<td>1.51</td>
<td>1.51</td>
</tr>
<tr>
<td>Cell M(_3)</td>
<td>1.12</td>
<td>1.12</td>
<td>.99</td>
<td>.90</td>
<td>1.00</td>
</tr>
<tr>
<td>Cell CU(_1)</td>
<td>1.21</td>
<td>1.28</td>
<td>1.04</td>
<td>.95</td>
<td>1.13</td>
</tr>
</tbody>
</table>

\(^1\) Values obtained by dividing width of the lunule by height. Values greater than 1 indicate oblate lunules.

One of the more consistent characters used in the study was the shape of the median black lunules of the ventral FW (forewing) in cells M\(_2\), M\(_3\), and CU\(_1\), but especially in M\(_3\) and CU\(_1\). The values given in Table 2 are averages obtained by taking measurements of each spot on every specimen using a binocular dissecting microscope with a micrometer disc grid in the eye-piece. These measurements of width and height of each individual spot were then adjusted to a ratio number by dividing width by height. Lunules that were oblate had numbers greater than one. Numbers near one or less indicated the lunules were not flattened and elongated.

Terminology used for describing veins, cells, and wing areas follows that given for butterflies in general and specifically for *Boloria* by Erhlich & Ehrlich (1961).

No consistent or reliable characters which could serve to differentiate subspecies were found in the genitalia.

*Boloria selene myrina* (Cramer)

(Figs. 2, 6)

*Papilio myrina* Cramer, 1777, vol. 2: 141, pl. 189, figs. B., C.

*Papilio myrinus*: Herbst, 1798.

*Argynnis myrissa* Godart, 1819, p. 253.


*Brenthis myrina nubes* Scudder, 1889, p. 595.

*Brenthis myrina* ab. *nubes*: McDunnough, 1938, p. 16.


Brenthis selene myrina: Clark, 1941, p. 384.
Brenthis selene marilandica Clark, 1941, p. 384.
Boloria myrina: dos Passos & Grey, 1945, p. 4.
Boloria selene marilandica: Klots, 1951, p. 89. dos Passos, 1964, p. 89.

**Diagnosis.** This subspecies is most closely allied to nebraskensis in coloration and pattern of markings. Series of the two are readily separated by size, since FW length of nebraskensis averages ca. 4 mm greater than myrina in both males and females.

The pattern of dorsal dark markings on the orange ground color of myrina is heavier than on nebraskensis and is comparable to atrocostalis (Huard). In the basal portion of the wings dorsally, myrina also has more dark scaling than nebraskensis, and the dark basal spot in the discal cell is frequently obscured with dark scales (ca. 30% of specimens). This spot is obscured in only 6% of nebraskensis specimens (Table 1). The black marginal band dorsally is a little heavier on myrina than nebraskensis.

In both subspecies, the black median lunules in cells M_2, M_3, and Cu_1 of the ventral FW tend to be elongated or oblate (Table 2). This tendency is less pronounced in myrina than in nebraskensis.

**Male.** Dorsal surface: ground color bright orange, with pattern of dark markings sharply demarcated; black wing margins of FW and HW not heavy, and enclosed row of orange marginal spots distinct and visible along entire margin; basal areas of both wings moderately dusted with dark scales, often obscuring basal spot in discal cell of HW.

Ventral surface: apical patch of FW solid cinnamon-brown, not infused with yellow scales; orange of FW ground color usually extending distally to cinnamon-brown apical patch without fading to yellow; black median lunules in cells M_2, M_3, and Cu_1 of FW oblate, elongated on long axis of wing; cinnamon-brown ground color of HW mostly solid, especially in basal area, with little dusting of yellow scales; postmedian row of light spots of HW all prominent and well silvered; anvil-shaped silver submedian spot in cell Cu_1 of HW seldom divided.

Length of forewing: 20.98 mm average.

**Female.** Similar to male but orange ground color of dorsal surface slightly more pale.

Length of forewing: 21.85 mm average.

**Type locality.** The type locality given by Cramer in his original description of myrina was New York. Cramer’s specimen most likely came from southeastern New York, rather than northern New York, which was probably quite inaccessible at that time.

Holland (1928) felt that specimens in his possession from Hunter and Saratoga, New York, Pennsylvania, and other localities in New England agreed with the somewhat crude figure given by Cramer and accepted the Hunter and Saratoga specimens as being toptotypical. Holland pointed out that the discal and basal markings of the wings on the upper side of these specimens were not as heavy as in Cramer’s original drawing and that they more nearly represented the “general run” of specimens in New England and the Middle States. He also mentioned that he had specimens from Hunter, New York and the Allegheny Mountains near Cresson, Pennsylvania that were as heavily marked as the specimen shown on Cramer’s plate. Specimens examined for this study from some localities, including Schuylkill Haven, Pennsylvania (Fig. 2) were similarly marked.

**Distribution.** Southern portions of New York, Vermont, and New Hampshire south to central Virginia and West Virginia, including Massachusetts, Rhode Island, Connecticut, New Jersey, Pennsylvania, Maryland, and Delaware, west through southern Michigan, extreme northeast Illinois, the southern portions of Wisconsin and Minnesota to eastern South Dakota (Fig. 1).
**Fig. 1.** Distribution of the subspecies of *Boloria selene* in North America.

**Remarks.** The subspecies *myrina* has been referred to by some authors (Klots, 1951; Shepard in Howe, 1975) as being average for the species in both size and markings. Because of this, many specimens representing intergrades between *atrocostalis* and *myrina* and between *myrina* and *nebraskensis*, as well as specimens of *nebraskensis* over much of its range, have been lumped together under *myrina*.

Specimens from central Ohio, northern Indiana, northern Illinois (except the extreme northeast corner), and Iowa previously considered to be *myrina* have been found to be *nebraskensis*. There is intergradation with *atrocostalis* along the entire northern limit of the range of *myrina*, and some evidence of intergrading with *nebraskensis* to the south in Illinois and northeastern Nebraska.

Two aberrations of *myrina* have been given names. Ab. *nubes* (Scudder) was described from a male collected in Sanbornton, New Hampshire, in which the median spots were enlarged and somewhat suffused. The type is now in the Museum of Comparative Zoology at Harvard. The name *nivea* (Gunder) was given to an albino male collected May 28, 1900, on Staten Island, New York. The ground color, both dorsal and ventral, is white, with no maculation change. The type is in the American Museum of Natural History.

The type locality of *marilandica* (Clark) is Beltsville, Maryland, “From the boggy pasture on the south side of the road from the Beltsville, Md. railway station to the Dept. of Agriculture experiment farm.” It is illustrated in Clark (1932, plate 3, figs. 5 & 6). The distinctive features listed in the original description were larger size, richer color, and heavier dark markings. There are no real consistent or significant differences between this local form (probably now extinct) and *myrina*, and it is here considered a synonym of *myrina*. The type is in the U.S. National Museum.

**Records.** The following records represent 193 typical specimens (130 ♂, 63 ♀) of *myrina* and additional intergrades examined:
myrina

CONNECTICUT: Fairfield, Hartford, and Windham cos. DELAWARE: Water Gap. MARYLAND: Baltimore and Garrett cos. MASSACHUSETTS: Hampshire and Norfolk cos. MICHIGAN: Indian Lake; Empire; Ramona; Cass, Delta, Jackson, Oakland, Ottawa, Van Buren, and Washtenaw cos. NEW JERSEY: Jamestown; Bergen, Hunterdon, Middlesex, Monmouth, Passaic, and Union cos. NEW YORK: Feurabush; E. Berne; Flushing; Ravenwood; McLean; New York City; Big Island; Somers; Fulton Co. PENNSYLVANIA: Lackawanna, Perry, and Schuylkill cos. RHODE ISLAND: Oak Lawn; Providence Co. SOUTH DAKOTA: Brown and Day cos. WISCONSIN: Douman; Milwaukee; Brown, Milwaukee, Ozaukee, Walworth, Washington, and Waukesha cos.

nr. myrina

ILLINOIS: McHenry Co. MASSACHUSETTS: Mt. Greylock; Readville; Berkshire Co. MICHIGAN: Presque Isle Co. VERMONT: Bennington Co. WISCONSIN: Waupaca Co.

Boloria selene nebraskensis (Holland)

(Figs. 2, 6)

Brenthis myrina var. nebraskensis Holland, 1928, p. 36; 1931, p. 105, pl. LV, fig. 8 (male type).
Brenthis myrina race nebraskensis: Leussler, 1938, p. 216.
Brenthis myrina nebraskensis: McDunnough, 1938, p. 16.
Brenthis selene nebraskensis: Clark, 1941, p. 384.

Diagnosis. Series of nebraskensis can be separated quite easily from the other subspecies of selene on the basis of large size alone, although other distinct features are present (Tables 1 & 2).

The dorsal wing margins of nebraskensis have the least amount of black of any of the subspecies, and the basal areas of both wings dorsally also have the least suffusion of dark scales. The basal spot in the discal cell of the dorsal HW is seldom completely obscured by dark scales (only 6% of the 398 specimens examined). The black median lunules in cells M2, M1a, and Cu1 of the ventral FW are oblate and elongated as in myrina, but in nebraskensis this tendency is more pronounced.

Male. Dorsal surface: ground color bright orange; normal pattern of dark markings very sharply demarcated; black margins of both wings reduced, and enclosed row of orange marginal spots very distinct, large, and visible along entire margin; very little suffusion of black scales at wing bases; basal spot in discal cell of HW almost never obscured by dark scales; postbasal spot in discal cell of HW relatively small, leaving space equal to at least one-half diameter of spot between spot and veins Rs and M2 above and below cell.

Ventral surface: ground color of FW very bright orange and usually extending completely to apical patch; apical patch bright cinnamon-brown, usually with little infusion of yellow scales; black median lunules in cells M2, M1a, and Cu1 of FW strongly oblate; slight dusting of yellow scales on cinnamon-brown ground color of HW in basal and limbal areas (postmedian band); postmedian row of light spots of HW all prominent and well silvered; anvil-shaped silver submedian spot in cell Cu1 of HW almost never divided.

Length of forewing: 24.78 mm average.
Fig. 2. Adults of *B. selene*: (a) *myrina* male, Schuylkill Haven, Schuylkill Co., Pa.; (b) same, ventral; (c) *myrina* male, New York City, N.Y.; (d) same, ventral; (e) *nebraskensis* male, Valley, Douglas Co., Neb.; (f) same, ventral; (g) *nebraskensis* male, Goose Lake Prairie State Park, Grundy Co., Ill.; (h) same, ventral. All photos natural size.
Female. Similar to male except orange of dorsal ground color slightly more pale. Length of forewing: 25.73 mm average.

Type locality. The type series consisted of four male specimens collected by Mr. E. A. Dodge. These specimens are presently at the Carnegie Museum in Pittsburgh. The type locality is Dodge Co., Nebraska.

Distribution. The range of nebraskensis is much more extensive than previous authors have reported. Typical specimens occur from east central Nebraska east through northern Iowa, northern Illinois, and northern Indiana to central Ohio (Fig. 1). It intergrades with myrina in some areas of the northern part of its range.

Remarks. B. s. nebraskensis was described by Holland in 1928 as a new variety of B. myrina. The sole basis for the name was the exceptional size of four male specimens collected by Mr. E. A. Dodge in Dodge Co., Nebraska. No description was given, except to call attention to size. Holland (1931) later discussed briefly nebraskensis in the revised edition of The Butterfly Book and illustrated a male type on Plate LV. Again, the only distinguishing character mentioned in the text was the large size.

My interest in nebraskensis was stimulated by discussion with Mr. Orville D. Spencer of Lincoln, Nebraska in 1968. Of particular interest was the fact that although good series of large typical specimens from Nebraska were present in some museums, none had been collected in recent years (Johnson, 1972).

I began actively seeking colonies of nebraskensis in Nebraska in the summer of 1968. That year colonies were located at Dead Timber State Recreation Area, Dodge Co., and Valley, Douglas Co. In 1969, several females taken from the Valley colony in July were kept alive and ova obtained. From these ova, 231 adult specimens (115 ♂, 116 ♀) were reared. Unfortunately, data on the immature stages were not kept, nor were photographs taken of the stages, nor were the stages studied in detail. The primary purpose of rearing was to obtain adult specimens.

In Nebraska, nebraskensis appears to have three broods per year; the first at the beginning of June from overwintering larvae, the second in mid-July, and the third in mid-August. Habitat where recent nebraskensis specimens were collected at Valley was wet meadow associated with river bottom and willow. Illinois habitats are similar (Conway, in litt.).

Records. Typical specimens of nebraskensis examined, including the reared Valley series, numbered 232 ♂ and 166 ♀. These records and additional intergrades are as follows:

nebraskensis


myrina/nebraskensis

NEBRASKA: Dodge and Madison cos.

In the western panhandle of Nebraska, extreme western South Dakota, southwestern North Dakota, and the northeastern prairie region of Colorado, specimens of selene exhibit characters which are different from nebraskensis. This area is isolated geographically and includes the major remaining conifer forest and montane areas of the Great Plains. Because of this geographic isolation and the differences observed in specimens from this area, the following new subspecies of B. selene is described.
Fig. 3. Adults of *B. selene*: (a) *sabulocollis* male, holotype, Smith Lake, Sheridan Co., Neb.; (b) same, ventral; (c) *sabulocollis* male, paratype, Timnath, Larimer Co., Colo.; (d) same, ventral; (e) *sabulocollis* male, paratype, Mineral Springs, Slope Co., N.Dak.; (f) same, ventral; (g) *tollandensis* male, Tolland, Gilpin Co., Colo.; (h) same, ventral. All photos natural size.
**Boloria selene sabulocollis** Kohler new subspecies  
(Figs. 3, 6, 7)

**Diagnosis.** This subspecies is intermediate in size between *myrina* and *nebraskensis*. The main characters separating it from *nebraskensis* and *myrina*, which it is quite similar to dorsally, are on the ventral wing surfaces. The median black lunules in cells $M_5$ and $C_u$ of the ventral FW are “square-shaped,” not oblate and elongated as in *myrina* and *nebraskensis*. There is more dusting of yellow scales on the cinnamon-brown ground color of the ventral HW of *sabulocollis*.

**Male.** Dorsal surface: normal pattern of dark markings sharply demarcated on orange ground color; row of orange marginal spots enclosed in black marginal band distinct and visible along entire margin of both wings, some suffusion of dark scales at wing bases, but basal spot in discal cell of HW seldom obscured; postbasal spot in discal cell of HW relatively small, leaving space equal to at least one-half diameter of spot between edge of spot and veins Rs above and $M_5$ below discal cell.

Ventral surface: ground color of FW dull orange, fading to yellow-orange before reaching apical patch; cinnamon-brown of apical patch dusted with yellow scales; black median lunules in cells $M_5$ and $C_u$ of FW “square-shaped,” not oblate and elongated; considerable dusting and infusion of yellow scales in cinnamon-brown ground color of HW, with row of black spots in postmedian cinnamon-brown band surrounded by halos of yellow scales, and infusion of yellow scales in basal area of all cells; anvil-shaped silver submedian spot in cell $Cu_1$ of HW almost never divided.

Length of forewing: 22.82 mm average; holotype 22 mm.

**Female.** Similar to male, but with orange of dorsal ground color slightly more pale.

Length of forewing: 23.75 mm average; allotype 25 mm.

**Types.** Holotype: male, Smith Lake, Sheridan Co., Nebraska, 1.viii.68, S. Kohler; placed in the collection of the American Museum of Natural History.

Allotype: female, same data as holotype; placed in the collection of the American Museum of Natural History.


Paratypes will be placed in the collections of the American Museum of Natural History, the Los Angeles County Museum, the National Museum of Natural History, the Allyn Museum of Entomology, J. S. Nordin, J. Oberfoell, J. R. Heitzman, R. E. Stanford, M. S. Fisher, and S. Kohler.

**Distribution.** The range of *sabulocollis* is limited to western Nebraska, the prairie region of northeastern Colorado, western South Dakota, and extreme southwestern North Dakota (Fig. 1). Specimens from Albany Co., Wyoming show intergradation between *sabulocollis* and *tollandensis*.

**Remarks.** A knowledge of the paleobotany of the western Great Plains is important in understanding how *sabulocollis* may have become isolated. Johnson (1975, 1976) points out that the present coniferous forests of the western Great Plains (Black Hills, Pine Ridge, Cheyenne Ridge, etc.) are the remains of extensive forest areas that once covered much of the region. The subspecies *sabulocollis* probably represents a relict of more extensive populations that were associated with the former coniferous forest.
Colonies in western Nebraska are situated at the marshy edges of lakes and adjacent wet meadows in the sandhills region, an area characterized by thousands of square miles of large, stabilized sand dunes covered with range grasses. The western part of this region, once covered by open pine-juniper forest, has abundant ground water, with many small lakes. Further east, the region becomes drier. The sandhills probably are an effective barrier to intergradation with *nebraskensis* to the east, although this possibility exists along the Platte and Elkhorn rivers. The colonies in southwestern North Dakota and western South Dakota are isolated from the east by extensive arid areas lacking suitable habitat.

The name *sabulocollis* is a combination of the Latin words for sand (sabulo) and hill (collis), which is descriptive of the area of the type locality.

*Boloria selene tollandensis* (Barnes & Benjamin)

(Figs. 3, 4, 7)

*Brenthis myrina tollandensis* Barnes & Benjamin, 1925, p. 44. Holland, 1928, p. 37.
*Brenthis myrina var. tollandensis*: Holland, 1931, p. 106.
*Brenthis selene tollandensis*: Clark, 1941, p. 384.
*Boloria myrina (=selene) tollandensis*: Brown, 1954, p. 64.

**Diagnosis.** This is the most lightly marked of the subspecies, with the pattern of dark maculation reduced dorsally, especially on the HW. Suffusion of dark scales in the basal areas of the wings dorsally is comparable to *atrocostalis*, and the basal spot in the discal cell of the dorsal HW is usually obscured by dark scaling. The postbasal spot in the discal cell of the dorsal HW is characteristically very large in relation to the cell, often filling almost the entire width of the cell. The size of this spot is accentuated by the otherwise fine maculation of the HW. Ventrally, *tollandensis* exhibits extensive infusion of yellow into the cinnamon-brown basal and discal areas of the HW.

**Male.** Dorsal surface: Ground color orange to yellow-orange; black marginal band reduced, and enclosed orange marginal spots very distinct and visible along entire margin of both wings; normal pattern of black markings reduced and narrow on both FW and HW, with exception of postbasal spot in discal cell of HW, which is enlarged and often fills almost entire width of cell, accentuated by otherwise fine markings of HW; considerable suffusion of dark scales at wing bases, especially on HW where dark scales form rather abrupt line across middle of discal cell, usually obscuring basal spot in cell.

Ventral surface: ground color of FW yellow-orange; apical cinnamon-brown patch of FW much reduced and powdery, with brown areas largely replaced by clear yellow-buff; black median lunules in cells M2 and Cu1 of FW “square shaped,” not oblate; extensive yellow scaling in HW, with cinnamon-brown of postmedian band between postmedian and submarginal rows of silver spots reduced to powdery patches between veins Rs and M2 and between veins M3 and Cu3, and remaining brown of basal area of HW powdered with yellow scales; anvil-shaped silver submedian spot in cell Cu2 of HW frequently divided (30% of specimens).

Length of forewing: 19.55 mm average.

**Female.** Similar to male but with orange of dorsal ground color noticeably more pale, especially on outer half of both FW and HW.

Length of forewing: 20.46 mm average.

**Type locality.** The type locality of *tollandensis* is Tolland, Gilpin Co. (not Moffat), Colorado. The original description (Barnes & Benjamin, 1925) lists Tol-
Fig. 4. Adults of *B. selene*: (a) *tollandensis* male, Avon, Cache Co., Ut.; (b) same, ventral; (c) *tollandensis/albequina* male, Moxee Bog, Yakima Co., Wash.; (d) same, ventral; (e) *tollandensis/albequina* male, Atlin, B.C.; (f) same, ventral; (g) *albequina* male, Homer, Alaska; (h) same, ventral. All photos natural size.

land as being in Moffat Co. This must be an error. The type series consisted of the holotype (♂), allotype (♀), and 12 paratypes (5 ♂, 7 ♀). All of these were in the Barnes collection, now at the U.S. National Museum.

**Distribution.** The range of typical *tollandensis* extends from north-central New
Mexico north through central Colorado and Wyoming, west through northeastern Utah, southern Idaho, and extreme southwestern Montana, and north through most of the Idaho panhandle.

**Remarks.** Nearly typical specimens have been examined from extreme northern Idaho. In eastern Oregon and Washington, and most of British Columbia, *tollandensis* intergrades with *albequina* (Holland) (Figs. 4 and 8). Intergrading with the eastern *atrocostalis* occurs over a wide band including most of Alberta and Montana, the eastern Idaho panhandle, and the northwest corner of Wyoming. Intergrading with *sabulocollis* occurs in eastern Wyoming.

Brown (1957) states that *tollandensis* in Colorado is single-brooded. Utah *tollandensis* appears to be double-brooded, and there is evidence that intergrades from Montana have two broods per year, since fresh adults have been collected from the same locality in both mid-June and mid-August.

Habitat listed by both Brown (1957) and Ferris (1971) for *tollandensis* in Colorado and Wyoming is willow bogs at rather high altitude, 9,000 to 10,000' for Colorado. The Utah specimens illustrated in Fig. 4 were taken at ca. 5500' elevation in an open boggy pasture near the mouth of a canyon. Montana specimens have been taken as low as 3300' in wet open meadows and river bottom near Missoula and at higher elevations in Glacier National Park and elsewhere in the state.

The aberration "serratimarginata" (Gunder) was described in 1926 from Vernon, British Columbia. The specimen, a male, was taken 12 August, 1904. The submarginal row of black markings of the dorsal HW are fused with the black marginal band, giving the margin a serrated appearance. The type is in the American Museum of Natural History (dos Passos, 1938).

**Records.** One hundred forty-one typical specimens (88 δ, 53 ♀) of *tollandensis* and additional intergrades were examined. Records of these specimens are as follows:

**tollandensis**

**COLORADO:** Rocky Mtn. Nat. Park; nr. Northgate; Boulder, Conejos, Gilpin, Grand, Lake, Routt, and Summit cos. **IDAHO:** Blaine, Fremont, and Latah cos. **MONTANA:** Beaverhead Co. **NEW MEXICO:** Rio Arriba and Sandoval cos. **UTAH:** Vineyard; Cache, and Utah cos. **WYOMING:** NE of Cora; Fremont, Johnson, and Sublette cos.

**nr. tollandensis**

**IDAHO:** Bonner and Custer cos. **OREGON:** Crook Co. **WYOMING:** Big Horn Mts.; Albany, Carbon, and Teton cos.

**albequina/tollandensis**

**BRITISH COLUMBIA:** Beaverfoot Range; Smithers; Atlin; Fernie; Lillooet; Robson; Cranbrook; and Laird Hot Springs. **WASHINGTON:** Yakima Co.

**atrocostalis/tollandensis**

**ALBERTA:** Didsbury; Banff; Carbon; Pine Creek; Bilby; and Slave Lake. **MONTANA:** Cascade, Flathead, Gallatin, Granite, Jefferson, Lake, Missoula, Ravalli, and Sweet Grass cos. **WYOMING:** Yellowstone Nat. Park; Park and Teton cos.

*Boloria selene albequina* (Holland)

(Fig. 4)

*Brenthis albequina* Holland, 1928, p. 40, figs. 4, 5, and 6; 1931, p. 107, pl. LV, figs. 19, 20, and 21 (types). McDunnough, 1932, p. 269; 1938, p. 16 (as synonym of *atrocostalis*).
Brenthis albequina var. baxteri Holland, 1928, p. 42.
Brenthis myrina atrocostalis ab. baxteri: McDunnough, 1938, p. 16.
Boloria selene albequina: dos Passos, 1964, p. 89.
Boloria selene albequina ab. baxteri: dos Passos, 1964, p. 89.

**Diagnosis.** Dorsally, *albequina* is similar to *atrocostalis*. Both have heavy dark wing margins, but *albequina* differs from *atrocostalis* in having a greater suffusion of dark scales in the basal areas of the wings (Table 1). There is also a tendency for the pattern of dark spots which are not obscured by the dark basal suffusion to appear “blurred” or “smudged,” not sharply demarcated as in *atrocostalis*.

The ventral surface of the HW of *albequina* also differs from that of *atrocostalis* in having considerable infusion of yellow scales into the cinnamon-brown of the basal and discal portions, as does *tollandensis*. In *atrocostalis*, these areas are largely solid cinnamon-brown.

**Male.** Dorsal surface: ground color of both wings dull orange; black marginal band heavy, and enclosed orange marginal spots obliterated on FW from apex posterior at least to cell M₃, and remaining spots on FW and HW reduced to small orange points; normal pattern of black markings heavy and usually appearing slightly “blurred” or “smudged,” not sharply demarcated; extensive suffusion of black scales into basal portions of wings, always obscuring basal spot in discal cell of HW and often postbasal spot, with suffusion forming more or less solid black patch on HW.

Ventral surface: ground color of FW dull yellow-orange; apical cinnamon-brown patch of FW much reduced and powdered with yellow scales, surrounded by dull yellow-buff; black median lunules in cells M₃ and Cu₅ of FW “square-shaped,” not oblate; considerable yellow scaling on HW, with cinnamon-brown of postmedian band between postmedian and submarginal rows of silver spots reduced and powdery; silver spot of postmedian band in cell M₃ of HW lacking, and spot in cell M₃ often indistinct; anvil-shaped silver submedian spot in cell Cu₅ of HW frequently divided (39% of specimens).

Length of forewing: 19.17 mm average.

**Female.** Similar to male.

Length of forewing: 20.08 mm average.

**Type locality.** This subspecies was described from seven males collected at White Horse Pass, Yukon Territory, by W. F. O. Baxter. The types are in the Carnegie Museum.

**Distribution.** The range of typical *albequina* is limited to southwest Alaska and adjacent portions of the Yukon Territory east into the far west portion of the Northwest Territories (Fig. 1).

**Remarks.** In northern British Columbia, *albequina* intergrades with *tollandensis*. Many British Columbia specimens have been incorrectly referred to as *albequina*. Specimens from Alberta, Montana, and northwestern Wyoming, many of which were also previously referred to as *albequina*, represent a wide band of intergradation between *tollandensis* and *atrocostalis*. These specimens exhibit dark wing margins dorsally, as in *atrocostalis*, but the pattern of markings is reduced as in *tollandensis*, especially on the HW. In addition, the postbasal spot in the discal cell is often enlarged, covering nearly the width of the cell in many specimens, as it does in *tollandensis*. Ventrally, the HW of these specimens exhibits characteristics of both *tollandensis* and *atrocostalis* (Figs. 5 and 8).

It has been suggested by some authors, as early as 1932 (McDunnough) and as recently as 1975 (Shepard, in Howe), that the name *albequina* be reduced to the synonymy of *atrocostalis*. It is my opinion that this decision is based primarily on the study of specimens from zones of intergradation with *atrocostalis* and *tollandensis* and that the name *albequina* should be used for the Alaska, Yukon, and Northwest Territories populations.

In the original description of *albequina*, Holland (1928) placed considerable emphasis on the anvil-shaped silver submedian spot in cell Cu₅ of the ventral HW.
Fig. 5. Adults of *B. selene*: (a) *atrocostalis* male, Lake Jacques Cartier, Laurentides Park, Que.; (b) same, ventral; (c) *atrocostalis/tollandensis* male, Florence, Ravalli Co., Mont.; (d) same, ventral; (e) *terraenovae* male, Doyle’s Station, Newfoundland; (f) same, ventral; (g) *terraenovae* male, Doyle’s Station, Newfoundland; (h) same, ventral. All photos natural size.
He pointed out the tendency of this spot to be divided in *albequina* and the inner half reduced in size. McDunnough (1932) felt that many of the other differences mentioned by Holland were due to the rubbed condition of the specimens and that the stress Holland placed on the division of the silver spot was unwarranted, since this condition was also present in specimens of *atrocostalis* from the north shore of the Gulf of St. Lawrence. Of 239 typical specimens of *atrocostalis* examined in this study, only 6% showed division of the submedian silver spot in cell \( Cu_2 \) of the ventral HW. This compares with the division of this spot being displayed in 39% of the specimens of *albequina* examined. Of 141 typical specimens of *tollandensis* examined, 30% had this spot divided. The tendency for the spot to be divided in both *albequina* and *tollandensis* and the extensive yellow scaling of the HW of both show that *albequina* is more closely allied to *tollandensis* than *atrocostalis*.

The name *baxteri* was given by Holland (1928) to an aberrant female of the same series as the types of *albequina* from White Horse Pass, Yukon Territory. The dark basal and median markings of the dorsal wing surfaces are enlarged and connected on this aberration.

**Records.** A total of 21 typical specimens (15 ♂, 6 ♀) of *albequina* were examined. This included a series that was examined for me by Mr. Kenelm Philip, Alaska Institute of Arctic Biology. The records are as follows:

**albequina**

**ALASKA:** Kenai Peninsula; Kodiak; Goldstream Valley, nr. Fairbanks; Chatanika River, NE of Fairbanks; nr. Talkeetna; and mile 154.7, new Anchorage-Fairbanks Hwy.

**nr. albequina**

**ALBERTA:** Laggan (Lake Louise).

*Boloria selene atrocostalis* (Huard)

(Figs. 5, 8)


*Brenthis myrina ab. jenningsae* Holland, 1928, p. 36.

*Brenthis myrina var. jenningsae*: Holland, 1931, p. 105, pl. LVI, fig. 9 (male type).

*Brenthis myrina atrocostalis ab. jenningsae*: McDunnough, 1932, p. 269; 1938, p. 16.

*Boloria selene atrocostalis ab. jenningsae*: dos Passos, 1964, p. 89.

*Brenthis selene atrocostalis*: Clark, 1941, p. 384.


**Diagnosis.** The subspecies *atrocostalis* is separated from *myrina* by the heavy dark marginal wing scaling dorsally, which often almost completely eliminates the normal row of orange marginal spots. It also has more suffusion of dark scales in the basal portions of the wings dorsally than does *myrina*, but not as much as *albequina*. Ventrally, the cinnamon-brown ground color of the HW of *atrocostalis* is not reduced or infused with yellow scales, as in *albequina*. The ventral FW median black lunules in cells \( M_1 \) and \( Cu_1 \) of *atrocostalis* are more "square-shaped," instead of oblate as in *myrina*.

**Male.** Dorsal surface: ground color bright orange; black marginal band heavy and broad, with enclosed orange marginal row of spots largely obscured by black, especially on FW, or completely obliterated by black on both FW and HW of
Fig. 6. Adults of B. selene: (a) myrina female, New York City, N.Y.; (b) same, ventral; (c) nebraskensis female, Valley, Douglas Co., Neb.; (d) same, ventral; (e) nebraskensis female, Goose Lake Prairie State Park, Grundy Co., Ill.; (f) same, ventral; (g) sabulocollis female allotype, Smith Lake, Sheridan Co., Neb.; (h) same, ventral. All photos natural size.
some specimens; normal pattern of black markings heavier, but sharply outlined on orange ground color; some suffusion of dark scales at bases of both wings, extending distally near inner margin of FW to median row of spots, and on HW filling ca. one-half of discal cell; basal spot in discal cell of HW usually obscured by dark scales.

Ventral surface: ground color of FW dull orange, extending to apical patch with no fading; apical patch of FW large, and solid cinnamon-brown in color, with little or no powdering of yellow scales; black median lunules in cells M, and Cu, of FW "square-shaped," not oblate; cinnamon-brown ground color of HW in basal portion and in postmedian band between postmedian and submarginal rows of silver spots solid, with little or no infusion of yellow scales; all postmedian light spots of HW prominent and well silvered.

Length of forewing: 20.08 mm average.

**Female.** Similar to male except orange ground color of dorsal surface slightly more pale and black dorsal wing margins less broad and heavy, with orange marginal row of spots more conspicuous.

Length of forewing: 20.57 mm average.

**Type locality.** The type locality of *atrocostalis* is Chicoutimi, Quebec.

**Distribution.** The range of *atrocostalis* extends from Nova Scotia west through Canada to western Saskatchewan and as far north as Churchill and Lynn Lake, Manitoba. In the United States, *atrocostalis* is found in Maine, most of Vermont and New Hampshire, the northern portions of New York, Michigan, Wisconsin, Minnesota, and in eastern North Dakota (Fig. 1).

**Remarks.** Huard (in Provancher & Huard, 1926) used the name *atrocostalis* at the species rank, but shortly after, McDunnough (1928) examined the type and found that it represented what he considered to be the eastern Canadian form of *myrina*. McDunnough then applied the name at subspecies rank to eastern Canada specimens.

The subspecies *atrocostalis* intergrades with *tollandensis* in Alberta, Montana, and northwestern Wyoming, with *albequina* in the northwestern part of its range and *myrina* along much of the southern limit of its range.

The name *jenningsae* (Holland) was applied in 1928 to an aberrant male specimen taken by Mrs. O. E. Jennings at Jellicoe, on Thunder Bay, Ontario. The transverse markings of the wings are fused and enlarged. The type is in the Carnegie Museum.

**Records.** Two hundred thirty-nine typical specimens (159 ♂, 80 ♀) and additional intergrades were examined:

*atrocostalis*

**MAINE:** Rangeley; E. Haepswell; Gilead; Seboomook Lake; Androscoggin, Penobscot, and Piscataquis cos. **MANITOBA:** Bereton Lake; Kelwood; Red Rock Lake; Brokenhead; Churchill; Betula Lake; Rennie; McCreary; Telford; and Riding Mts. **MICHIGAN:** Cheboygan, Chippewa, Emmet, Ostego, and Schoolcraft cos. **MINNESOTA:** Arago; Aitkin, Anoka, Cass, Cook, Crow Wing, Dakota, Lake, Otter Tail, St. Louis, Sherburne, and Rice cos. **NEW BRUNSWICK:** Edmundston; St. Leonard; and Dorchester. **NEW HAMPSHIRE:** Randolph; Jefferson; Belknap, Carrol, Coos, and Grafton cos. **ONTARIO:** Nakina; Hymers; Savanne; Nipigon; Nipigon Lake; One Sided Lake; Upsala; Poland; Geraldton; Sudbury; Wabigoon; Guelph; Goodwood; Toronto; Charlton; and Blind River. **QUEBEC:** Montreal; Casapeda River; Lytton; Lanoriae; Laval; Lomininque; Bois de Filion; Laurentides Park; St. Calixte de Kilkenny; Metapedia; Ste. Flavien; and St. Agapit. **SASKATCHEWAN:** Rivercourse and Lloydminster. **VERMONT:** Caledonia and Windsor cos. **WISCONSIN:** Chippewa, Dunn, Forest, Lincoln, Marathon, Oneida, Price, and Sawyer cos.
Fig. 7. Adults of *B. selene*: (a) *sabulocollis* female, paratype, Timnath, Larimer Co., Colo.; (b) same, ventral; (c) *sabulocollis* female paratype, Mineral Springs, Slope Co., N.Dak.; (d) same, ventral; (e) *tollandensis* female, Tolland, Gilpin Co., Colo.; (f) same, ventral; (g) *tollandensis* female, Avon, Cache Co., Ut.; (h) same, ventral. All photos natural size.
Boloria selene terraenovae (Holland)
(Fig. 5)


Brenthis myrina var. terraee-novae: Holland, 1931, p. 105, pl. LV, fig. 13 (male type).

Brenthis selene terraee-novae: Clark, 1941, p. 384.
Boloria selene terraee-novae: Klots, 1951, p. 89.

Diagnosis. The dorsal wing surfaces of the majority of terraenovae specimens are much like myrina. The wing margins are not as heavily marked with black scales as are those of atrocostalis. Basal suffusion of dark scales is a bit heavier than in myrina, but few specimens approach the degree of suffusion in Holland’s types.

The ventral surfaces of the HW are a different shade of brown, being consistently a deep, bright mahogany rather than the cinnamon-brown of the other subspecies. Occasionally, specimens of atrocostalis will approach this mahogany color of the HW, but have the heavier black wing margins characteristic of that subspecies.

Male. Dorsal surface: ground color bright red-orange; black marginal band not heavy, and enclosed orange marginal row of spots visible along entire margin of both wings in most specimens; normal pattern of black markings sharply demarcated on ground color; suffusion of dark scales in basal areas of both wings, in HW filling ca. one-half of discal cell; basal spot in discal cell of HW almost always obscured by dark scales.

Ventral surface: ground color of FW deep orange, usually extending to apical patch with little or no change in color; apical patch of FW not reduced, and solid bright mahogany-brown, with no powdering of yellow scales; ground color of HW uniform deep, bright mahogany, and solid, with little or no infusion of yellow scales; yellow areas of HW more or less restricted to cells Rs, M1, M3, and Cu1 in area between submedian and postmedian rows of silver spots and to normal patch in cells M1 and M3 just basad of submarginal row of silver spots; row of black limbal spots on HW overlaid with mahogany scales, with mahogany color masking black so that spots appear dark brown; all postmedian silver spots prominent, except spot in cell M2, which is reduced in most specimens.

Length of forewing: 20.67 mm average.

Female. Similar to male, but orange of dorsal ground color more pale.

Length of forewing: 21.50 mm average.

Type locality. The type locality of terraenovae is listed only as Newfoundland. Mr. C. F. dos Passos (1935) examined the holotype and two paratypes and commented that, although the labels did not show from what area of Newfoundland they came, it was probably the eastern part of the island. The types are in the Carnegie Museum.

Distribution. The range of terraenovae is limited to the Island of Newfoundland.

Remarks. In Nova Scotia and possibly New Brunswick, terraenovae intergrades to some extent with atrocostalis. Boloria selene have been recorded from Labrador, and these may represent neither terraenovae nor atrocostalis, but too few specimens are available to make sound judgments.

In the original description by Holland (1928), the only distinguishing factor mentioned was that the inner halves of both wings were suffused dorsally by dark scales, obscuring the wing markings in these areas. Such specimens are not representative of the normal run of specimens from Newfoundland, as evidenced by the specimens examined for this study. In 1935, dos Passos reached similar conclusions.
Fig. 8. Adults of *B. selene*: (a) *tollandensis/albequina* female, Moxee Bog, Yakima Co., Wash.; (b) same, ventral; (c) *atrocostalis* female, Lytton, Que.; (d) same, ventral; (e) *atrocostalis/tollandensis* female, Florence, Ravalli Co., Mont.; (f) same, ventral. All photos natural size.

when he examined a series of 32 males and 11 females from Newfoundland and compared them with the types. He found that some specimens were as heavily marked with dark scales in the basal wing areas but that most of the specimens were not.

**Records.** Fifteen typical specimens (14 ♂, 1 ♀) of *terraenovae* were studied. These records and additional intergrades are as follows:

*terraenovae*

**NEWFOUNDLAND**: Doyle's Station; Codroy; and Spruce Brook.

*nr. terraenovae*

**NOVA SCOTIA**: Mt. Uniacke; Port Shoreham; and Passboro.
Conclusions

Although *Boloria selene* is quite variable in both size and markings, several recognizable and consistent populations exist within its range in North America. There is considerable intergradation among these populations at the limits of their ranges. Over the course of this study, the ranges of these recognizable populations have been more precisely defined, as have the zones of intergradation among populations.

In general, *selene* in North America exhibits a gradual intergradation of characters throughout its range, more evident on north-south lines, but also present on east-west lines. Names are available to apply at subspecific rank to populations sufficiently differentiated on these clines, and are useful tools when so applied. It is felt that the existence of these clines has not been obscured by the recognition of too many subspecies names and that those names recognized in this paper best portray the population changes on the clines.

In the west, typical *tollandensis* from the mountains of central Colorado and New Mexico form the southern pole of a cline and gradually intergrade into *albequina* in southwestern Alaska at the northern pole of the cline. A quite variable intermediate population occurs in a broad band including eastern Oregon and Washington, most of British Columbia, Alberta, northern Idaho and Montana, and northwestern Wyoming. This intermediate population is influenced by intergrading from the east, by *atrocostalis* on the north and *sabulocollis* to the south. Specimens from much of this intermediate population may show characteristics predominantly of *tollandensis*, *albequina*, or *atrocostalis*, or characteristics that are intermediate.

In the western Great Plains, a relict population (*sabulocollis*), which probably became isolated as coniferous forest began its demise in this area, has been newly described.

In the east, the north-south intergradation is more stepped and closely parallels environmental factors, chiefly habitat. The northern population (*atrocostalis*) of the coniferous boreal forest zone intergrades into the central population (*myrina*), associated with the deciduous eastern forest zone, and then into the southern population (*nebraskensis*) of the prairie zone, which has never supported forests.

On the east coast, the population named *marilandica* is a local phenotypic expression influenced by habitat similar to that of *nebraskensis*. The *marilandica* population is restricted to a prairie habitat of the lower coastal plain in Maryland, while *myrina* is present in the piedmont and deciduous forest zones. Because it is a local phenotypic population
differing only slightly from myrina, marilandica has been relegated to the synonymy of myrina.

A weaker east-west cline is formed by terraenovae and atrocostalis in the northeastern portion of the range of selene. The name terraenovae is retained to apply to the sufficiently differentiated eastern pole of this cline.

Through application of this gradual intergradation concept, ranges of some selene populations have been significantly expanded (nebraskensis and tollandensis), while others have been reduced (albequina and myrina).

As a result of this study, the following treatment of Boloria selene in North America is proposed:

Boloria selene (Denis & Schiffermüller), 1775

a. s. myrina (Cramer), 1777
   myrinus (Herbst), 1798
   myrissa (Godart), 1819
   ab. "nubes" (Scudder), 1889
   ab. "nivea" (Gunder), 1928
   marilandica (Clark), 1941
b. s. nebraskensis (Holland), 1928
c. s. sabulocollis Kohler, 1977
d. s. tollandensis (Barnes & Benjamin), 1925
   ab. "serratimarginata" (Gunder), 1926
e. s. albequina (Holland), 1928
   ab. "baxteri" (Holland), 1928
f. s. atrocostalis (Huard), 1927
   ab. "jenningsae" (Holland), 1928
g. s. terraenovae (Holland), 1928

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